

Devonian Syringostromatid Stromatoporoids from the Broken River Region, North Queensland

BARRY D. WEBBY*¹ AND YONG YI ZHEN²

¹ Centre for Ecostratigraphy & Palaeobiology,
Department of Earth & Planetary Sciences, Macquarie University, NSW 2109, Australia
bwebby@laurel.ocs.mq.edu.au

² Australian Museum, 6 College Street, Sydney NSW 2010, Australia
yongyi.zhen@austmus.gov.au

ABSTRACT. Six species of syringostromatid stromatoporoids are described from the biostratigraphically well-constrained carbonate successions of the Broken River region, North Queensland; the various occurrences range from earliest Devonian (early Lochkovian) to Mid-Devonian (late Eifelian). Included are three new Lochkovian species, *Atopostroma stearni* from the uppermost part of the Jack Formation and the Martins Well Limestone Member of the succeeding Shield Creek Formation, *A. protentum* and *Habrostroma alternum* also from the Martins Well Limestone Member. Transitional forms between the species of *Atopostroma* and *Habrostroma* are recorded from the Martins Well fauna. In addition *Atopostroma distans* (Ripper, 1937) is found in the Lomandra Limestone (late Emsian), and is present in reworked pebbles of the Dip Creek and the Chinaman Creek limestones of possible late Emsian-Eifelian. Sparse records of *Columnostroma* sp. in the Mid-Devonian (late Eifelian) Dosey Limestone, and reworked clasts of *Parallelopora* sp. in the Chinaman Creek Limestone, also occur. Characteristic structural elements of syringostromatid fauna are described including pachysteles, pachystromes and microlaminae, and microreticulate (acosmoreticular and clinoreticular) microstructures in the best preserved specimens. Also aspects of the evolutionary development of the fauna and the nature of the preservation of certain structural elements are discussed.

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This contribution is the second documenting the morphological features of the Devonian stromatoporoids of the Broken River region, North Queensland (Fig. 1), this time focusing almost entirely on descriptions of the syringostromatid fauna. The earlier work of Webby & Zhen (1997) was devoted to describing 31 species, representing more than half the orders of the class Stromatoporoidea from the region, namely the labechiids, actinostromatids, clathrodictyids and stromatoporellids. One of these described stromatoporellids was a dendroid species, *Stachyodes costulata* Lecompte, 1952, from the late Givetian or Frasnian

Stanley Limestone Member of the Mytton Formation of the SD192S section of the Broken River region, now also assigned to the syringostromatids.

The only other significant contribution on Devonian stromatoporoids of North Queensland since our earlier (1997) publication is that of Cook (1999) describing 35 stromatoporoid taxa from the Middle Devonian Fanning River Group of the Burdekin Basin, from an area about 180 km to the east (Fig. 1). Included are descriptions of a number of Middle Devonian (Givetian) syringostromatids—two species of *Coenostroma*, *C. burdekinense* Cook, 1999, and

* author for correspondence

C. wyatti Cook, 1999, a species left in open nomenclature that was ambiguously recorded as a *Parallelostroma* or *?Parallelopora* (Cook, 1999, p. 542), and four species of *Stachyodes*, namely, *S. crassa* Lecompte, 1952, *S. costulata* Lecompte, 1952, *S. sp. A*, and *S. sp. B*.

Stratigraphic distribution

All the Devonian syringostromatids known from the Broken River region are described herein, except for the species of *Stachyodes* mentioned above. They comprise *Atopostroma distans* (Ripper, 1937), *A. stearni* n.sp., *A. protentum* n.sp., *Habrostroma alternum* n.sp., *Columnostroma* sp. and *Parallelopora* sp.

In terms of the stratigraphic succession (Figs 1–2), the occurrence of *Atopostroma stearni* n.sp. in the topmost part of the Jack Formation (upper limestone member) at the western end of the Broken River Gorge (Grid reference: 7859-655455) is the earliest record of the genus in Australia from a horizon that is very close to the Silurian–Devonian boundary, most probably earliest Lochkovian in age (Jell *et al.*, 1993, p. 240) rather than latest Pridoli. *Atopostroma stearni* ranges up into the Martins Well Limestone Member of the Shield Creek Formation, occurring through a 35 m interval above the base of the NE–SW orientated MW section at Martins Well (Grid reference: 7859-685684; see Fig. 1), of late Lochkovian–early Pragian age. Another species of *Atopostroma*, *A. protentum* n.sp. occurs through the same interval, and a species of *Habrostroma*, *H. alternum* n.sp., is associated, though it has a more restricted distribution within the lower, 1–8 m thick, interval (late Lochkovian) of the Martins Well Limestone Member. These Martins Well species of *Atopostroma* and *Habrostroma* are of interest in exhibiting a range of transitional forms, especially between *A. protentum* and *H. alternum*. Stearn (1993, p. 221) has previously commented on this relationship, though he made the comparison with *Parallelostroma* rather than *Habrostroma*. The particular species has the characteristic acosmoreticular microstructure of *Habrostroma*. No species of *Parallelostroma* with a typical orthoreticular microstructure are known from the Broken River region.

Another species of *Atopostroma*, *A. distans* (Ripper, 1937), is described from the Broken River succession but from higher in the succession, through a 64 m thick interval within the Lomandra Limestone of late Emsian age in the SD170 section (Grid reference: 7858-611408; Fig. 1). One illustrated specimen of the species from this locality is exceptionally well preserved (see Fig. 3A, C–D, F). The species is also present in reworked pebbles of both the Dip Creek and Chinaman Creek limestones, of probable late Emsian or Eifelian age. *Atopostroma distans* has a wide distribution in eastern Australia in Victoria and central New South Wales. In the type locality in eastern Victoria it occurs in the Buchan Caves Limestone of early Emsian age (Webby *et al.*, 1993). It has been claimed to have a much wider distribution, with the occurrences recorded by Stearn (1983), and Prosh & Stearn (1996) from the Emsian of Arctic Canada and the Yukon seeming to be genuinely conspecific, but May's (1999, 2005) suggestion that *A. distans* is a junior synonym of the poorly preserved *Atopostroma frustulum* (Počta, 1894) from the Pragian of the Czech Republic is unacceptable given its coarser microreticular patterns and thicker pachysteles.

Other syringostromatid material collected from the Broken River region is rather limited and poorly preserved. *Columnostroma* sp. has been recorded from the Dosey Limestone (upper Eifelian), 11 m above the base in the SD260 section, from 2 km NNW of Storm Hill (Grid reference: 7858-548407), and *Parallelopora* sp. is reported from reworked pebbles of the Chinaman Creek Limestone (Grid reference: 7859-690601), having an uncertain, possibly late Eifelian age.

Background of previous work

Stearn (1980) proposed a new classification of Palaeozoic stromatoporoids that employed the structural elements as the main diagnostic features for the subdivision of the group. In that classification he introduced the new order Stromatoporida Stearn, 1980, comprised of three families—the Stromatoporidae, Syringostromellidae and Syringostromatidae—these groups being differentiated mainly on the differences in their amalgamated networks of longitudinally directed, wall-like elements termed pachysteles, and tangentially aligned layers called pachystromes and one or more thin laminae or microlaminae (Stearn, 2007, p. 559). In his new classification, Stearn (1980) preferred to minimize the emphasis on microstructures for higher-level classification because of the pervasive influence of diagenesis in changing the original state of stromatoporeid skeletons, thus making them difficult to apply.

However, Stearn (1993) in his major revision of the order Stromatoporida, while continuing to recognize the importance of structural elements, acknowledged as equally significant the cellular and microreticulate microstructures that were present across the group as a whole, with cellular microstructures in genera belonging to the families Stromatoporidae and Syringostromellidae, and microreticulate microstructures confined to the genera of family Syringostromatidae. The earlier contributions on the nature and origins of microreticular microstructures by Parks (1909, 1936), Kaźmierczak (1971), Nestor (1974) and Stock (1989) helped to explain how microreticulate microstructures may have originated, and how they could be used in classifying the group. Microstructural differences were fundamentally important in differentiating between the two groups and the order Stromatoporida Stearn, 1980 was polyphyletic. Consequently, Stearn (Stearn, 1993; Stearn, *in* Stearn *et al.*, 1999) redefined the order Stromatoporida to include only the genera exhibiting a cellular microstructure, and order Syringostromatida Bogoyavlenskaya, 1969 was reinstated as a name to encompass the genera with a microreticulate microstructure—though Bogoyavlenskaya's (1969, p. 21) original diagnosis of Syringostromatida made no mention of microstructure, and adopted a different conception with inclusion of some stromatoporellid family groups. In terms of origins, Stearn (1993) suggested that two orders arose independently during the Early Silurian (Llandovery) from different stocks—the revised order Stromatoporida derived from the Clathrodictyida, and the restored order Syringostromatida, from the Actinostromatida, or at least from one of its families, the Densastromatidae Bogoyavlenskaya, 1974.

Only one family, the Syringostromatidae Lecompte, 1952, was initially included in the order Syringostromatida (Stearn, 1993), but the classification has been successively

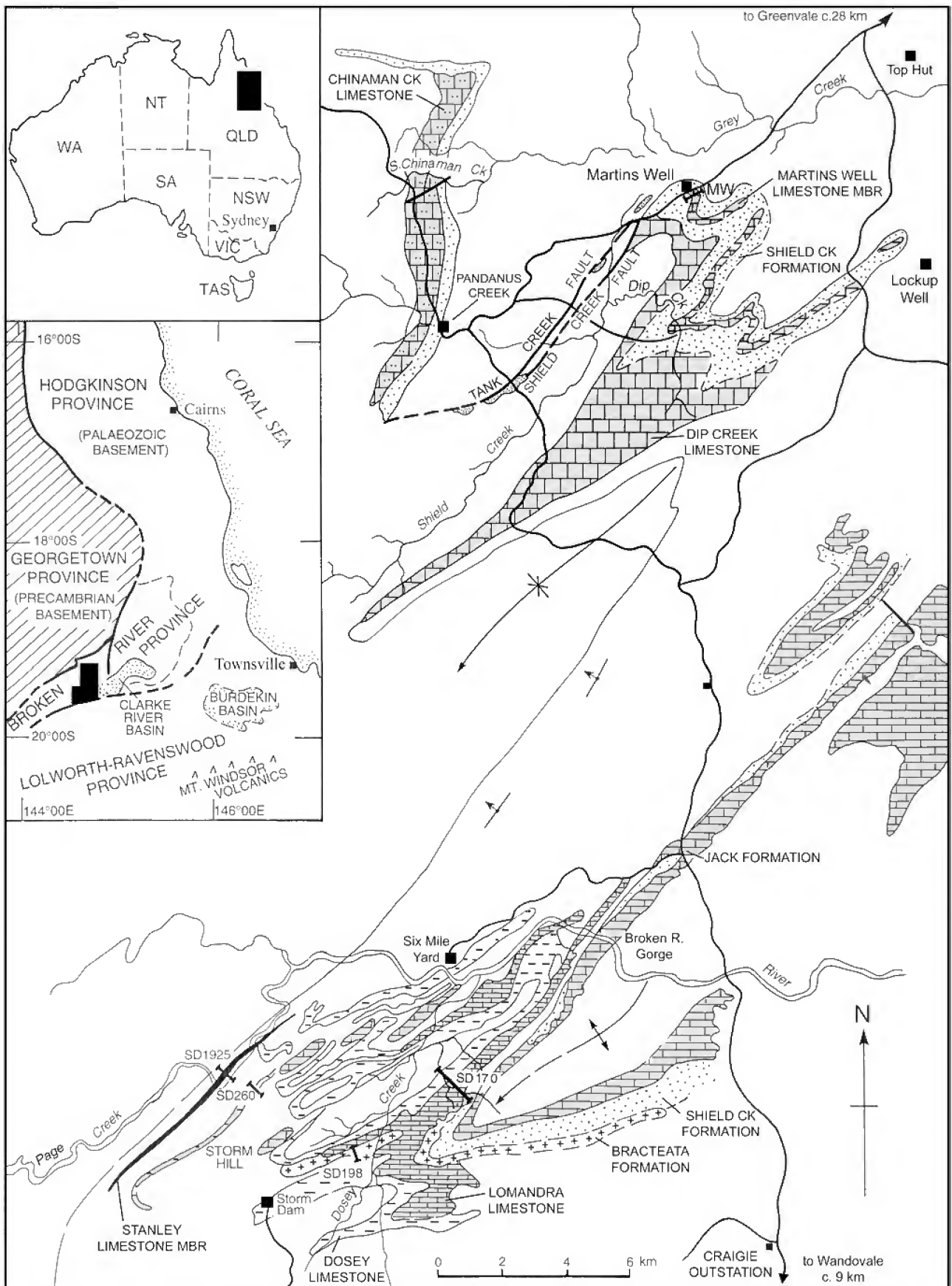


Fig. 1. Map of the Broken River region, north Queensland, showing the main areas of exposure of Upper Silurian and Devonian carbonate rocks, and locality data including identification of stratigraphic units and location of sections bearing the stromatoporoids described herein. Sources of geological mapping are after Withnall *et al.* (1988); Withnall & Lang (1993), with additions including location of SD and MW sections after Mawson *et al.* (1988), Mawson & Talent (1989), and Sloan *et al.* (1995).

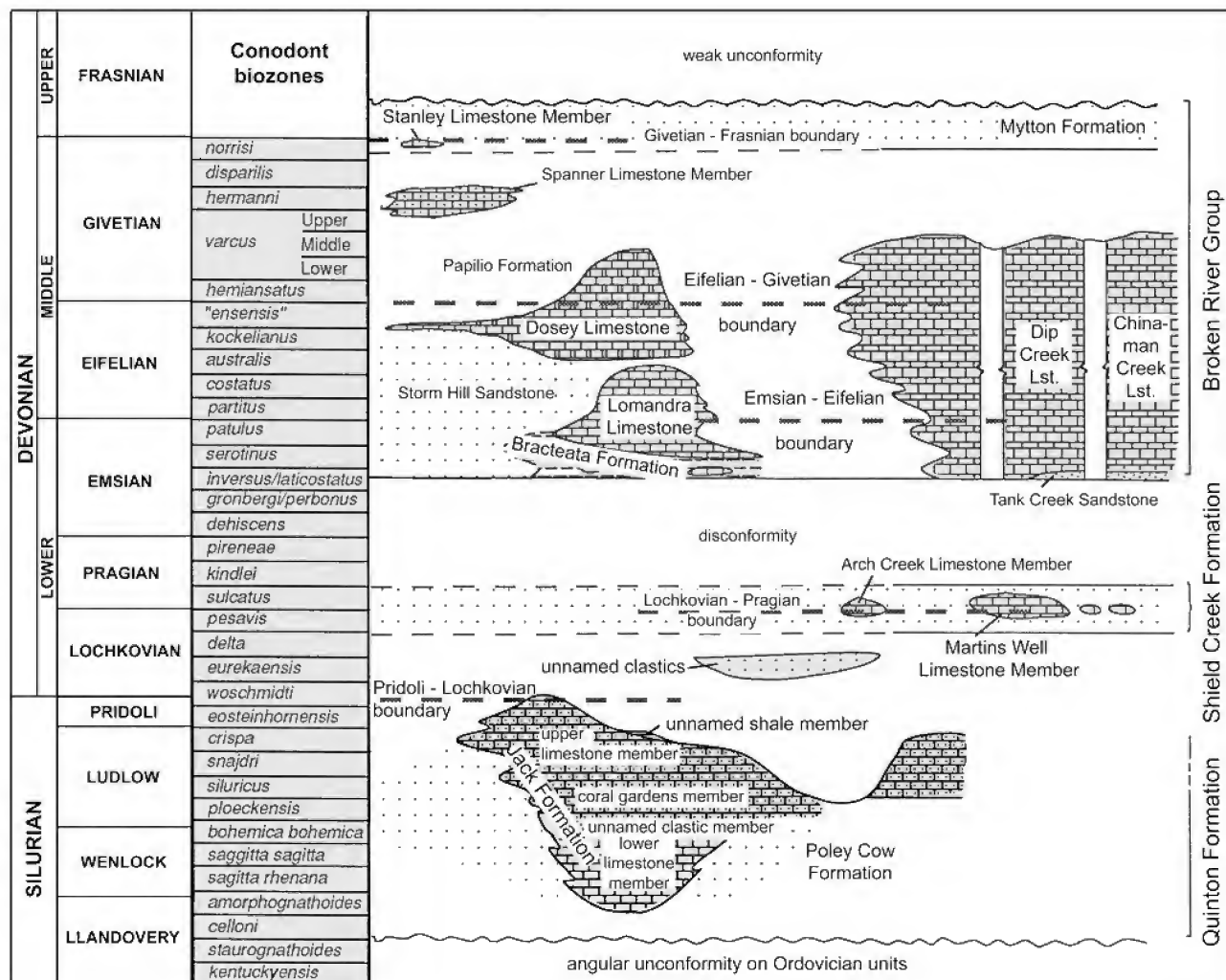


Fig. 2. Stratigraphic chart to illustrate the age relationships of the Silurian to Devonian successions across the Broken River region of North Queensland, from northern to southern parts of the area (that is, from right to left sides of chart), based on conodont data presented in Mawson *et al.* (1988), Mawson & Talent (1989), and Sloan *et al.* (1995; see especially text-fig. 3).

modified by Stearn in more recent years, in line with his evolving views, to a subdivision into three families—the Syringostromatidae, Coenostromatidae Waagen & Wentzel, 1887, and Stachyoditidae Khromykh, 1967 (see Stearn, *in Stearn et al.*, 1999). Then, in the hypercalcified sponge volume of the *Treatise on Invertebrate Paleontology* volume, Stearn (in press) excluded the name Syringostromatidae, in favour of a revised and enlarged Coenostromatidae, and the addition of family Parallelostromatidae Bogoyavlenskaya, 1984. What has become crucially important in syringostromatid classification is the nature of the microreticulate microstructure, though it does not by itself define the group.

Three different kinds of microreticulate microstructure have been recognized within pachystele and pachystromal elements of the syringostromatids by Stock (1989), and in Stearn *et al.* (1999—see definitions on p. 8 therein). These comprise: (a) regular longitudinally aligned grid-like patterns (orthoreticular); (b) upwardly diverging patterns (clino-reticular); and (c) irregularly arranged (acosmoreticular), patterns of micropillars and microcolliculi, with sometimes the latter two types being gradational between each other. In the latest version (in the unpublished *Treatise* volume), Stearn (in press) includes a classification of syringostromatids, with

the coenostromatid genera usually characterized by showing clinoreticular and/or acosmoreticular microstructure, and the parallelostromatid genera typically exhibiting an orthoreticular microstructure. In that contribution, Stearn assigns a total of eight genera—the coenostromatids *Atopostroma*, *Coenostroma*, *Columnostroma*, *Habrostroma* and *Syringostroma*, the parallelostromatids *Parallelostroma* and *Parallelopora*, and the stachyoditid *Stachyodes*—to the order Syringostromatida.

In terms of the origins of the Syringostromatida, Stearn (1993, pp. 208–210) has recognized that it is likely that the group arose from the family Densastromatidae of the order Actinostromatida. A number of morphological resemblances have been noted between the two major groups. Though the characteristic patterns in actinostromatids of coarse-textured, hexactinellid-type, skeletons with long pillars and beam-like colliculi, as well as a compact microstructure, (Stearn, *in Stearn et al.*, 1999), are features not shared by syringostromatids, the finer-textured, “microreticulated” skeletons composed of micropillars and microcolliculi (Stock & Burry-Stock, 1998; Stock, *in Stearn et al.*, 1999), do resemble the microreticulate microstructures of syringostromatids. However, these densastromatid structures are strictly small-scale primary skeletal elements, rather than

microstructures that form amalgamated nets within the larger primary macrostructural elements of syringostromatids, that is, within their pachysteles and pachystromes (Stearn, 1993; Stearn, in Stearn *et al.*, 1999).

Stearn (1993, p. 210) and Stearn *et al.* (1999, p. 51) suggested that the Syringostromida arose from the Actinostromatida (specifically the densastromatids) during the Early Silurian, and that the actinostromatid genus *Plectostroma* Nestor, 1964, may have been the rootstock to the finer-textured densastromatid lineage that first evolved early in the Wenlock. The syringostromatid genus *Parallelostroma* Nestor, 1966 was considered to have descended later from that densastromatid stock, probably in the late Wenlock. Stearn (1993, text-fig. 4) interpreted *Parallelostroma* as ancestral to most of the Early-Mid Devonian, syringostromatid genera, but it exhibits an orthoreticular microstructure that contrasts with the dominantly clinoreticular and acosmoreticular microstructures of the majority of Early-Mid Devonian genera. It seems likely that the integrity of individual microstructural types would have been retained within lineages through time. Therefore, an alternative viewpoint is proposed namely, that the Devonian genera evolved independently from other lines of descent during the Silurian, probably from another densastromatid, or a pseudolabechiid, descendant lineage with ancestral acosmoreticular and clinoreticular microstructures (Nestor, 1974; Stock & Burry-Stock, 1998, Stock, in Stearn *et al.*, 1999).

In the Broken River region, close relationships exist between the genera *Habrostroma* and *Atopostroma*, given they both exhibit acosmoreticular and clinoreticular microstructures, and show transitional relationships at the species level across both genera within the late Lochkovian-early Pragian Martins Well Limestone Member, as described herein. Neither appears to have been derived from an orthoreticulate genus like *Parallelostroma*, though more work needs to be done to properly reassess whether all Late Silurian species described as *Parallelostroma* are truly members of this genus. The genus *Habrostroma*, for example, based on *H. kaugatomicum* (Riabinin), has been confirmed from Upper Silurian (Pridoli) successions in New York and Virginia, USA (Stock, 1989, fig. 2E,F), but this same Pridolian species in Estonia (see Nestor, 1999) has been retained as a species of *Parallelostroma*. The genus *Atopostroma* appears in the earliest Devonian (early Lochkovian), as demonstrated here by the first occurrences of *A. stearni* in the uppermost part of the Jack Formation in the Broken River region, and the same species occurs in Arctic Canada, perhaps a little later, in the late Lochkovian (Stearn, 1990), that is, from an equivalent stratigraphic interval to that sampled at Martins Well where the range of transitional forms between *Atopostroma* and *Habrostroma* occur. Not only are there transitional forms associated with *A. protentum* and *H. alternum* in the Martins Well section, but specimens of *A. stearni* also showing gradational tendencies to *A. protentum* and *H. alternum* in that section. It seems possible therefore that, though *Atopostroma* may have evolved from *Habrostroma* at the beginning of the Devonian, a range of transitional morphologies may have existed throughout Lochkovian time, or alternatively these gradational changes across two genera may be more related to differences in preservational types. Only by collecting and studying large numbers of samples of these taxa in Lochkovian sequences elsewhere will it be possible to test these alternative suggestions.

Systematic palaeontology

The majority of stromatoporoid specimens used in this study have been collected by Webby, and precisely located in the measured sections of J.A. Talent, R. Mawson and colleagues from Macquarie University. In addition the specimens are positioned with respect to the grid references contained on the 1:100 000 Broken River Special geological map of Withnall & Lang (1992), and the Queensland 1:100 000 Topographic Map Sheets 7858 (Wando Vale) and 7859 (Burges). This material has been designated Australian Museum (AM F.) catalogue numbers for the type and figured specimens (hand specimens) with a separate set of registration numbers (AM FT. numbers) for each individual thin section, in most cases allocated on the basis of two numbers for each specimen, representing pairs of longitudinally and tangentially orientated thin sections of each specimen. Other Broken River samples were collected by C.W. Mallett in the 1960s and some of these were used in the present descriptions. The specimens were catalogued by Mallett using the prefix UQF and registered by their locality numbers using the prefix UQL; all the material was housed in the Geology Department of the University of Queensland, and now in the Queensland Museum.

The terms pachystele, pachystrome and allotube (Stearn, 2007, p.559; Stearn, in Webby *et al.*, in press, in the "Glossary" of the forthcoming *Treatise* volume on hypercalcified sponges) are used in this contribution in preference to terms coenosteole, coenostome and coenotube, as defined previously in Stearn *et al.* (1999, p.5); these latter are no longer recommended for use because the terms have connotations with common colonial forms like cnidarians.

Class Stromatoporoidea

Nicholson & Murie, 1878

Order Syringostromatida

Bogoyavlenskaya, 1969

Family Coenostromatidae

Waagen & Wentzel, 1887

Atopostroma Yang & Dong, 1979

Type species. *Atopostroma tuntouense* Yang & Dong, 1979.

Diagnosis: Pachysteles (pillars, in poorly preserved condition) moderately thick, superposed, inverted conical to post- and spool-shaped; microstructure usually microreticular. Pachystromes (seem to be laminae in less well preserved state) are laterally extensive and variably thickened; differentiated into thin, sharply defined, flattened, laterally persistent, microcolliculate bounding microlamina at top and, where well enough preserved, underlain by irregularly spread network of microreticular material that joins pachysteles, and may include other close-spaced, but more discontinuous, microlaminae; pachystrome floors irregular, best defined in dome-shaped contacts over galleries. Dissepiments rare, widely scattered, either small cyst-like, or long, wavy, microlamina-like plates. Microreticular structure of skeleton composed of variable fine network of micropillars and microcolliculi in microlaminae; in tangential section microstructures composed of acosmoreticular material;

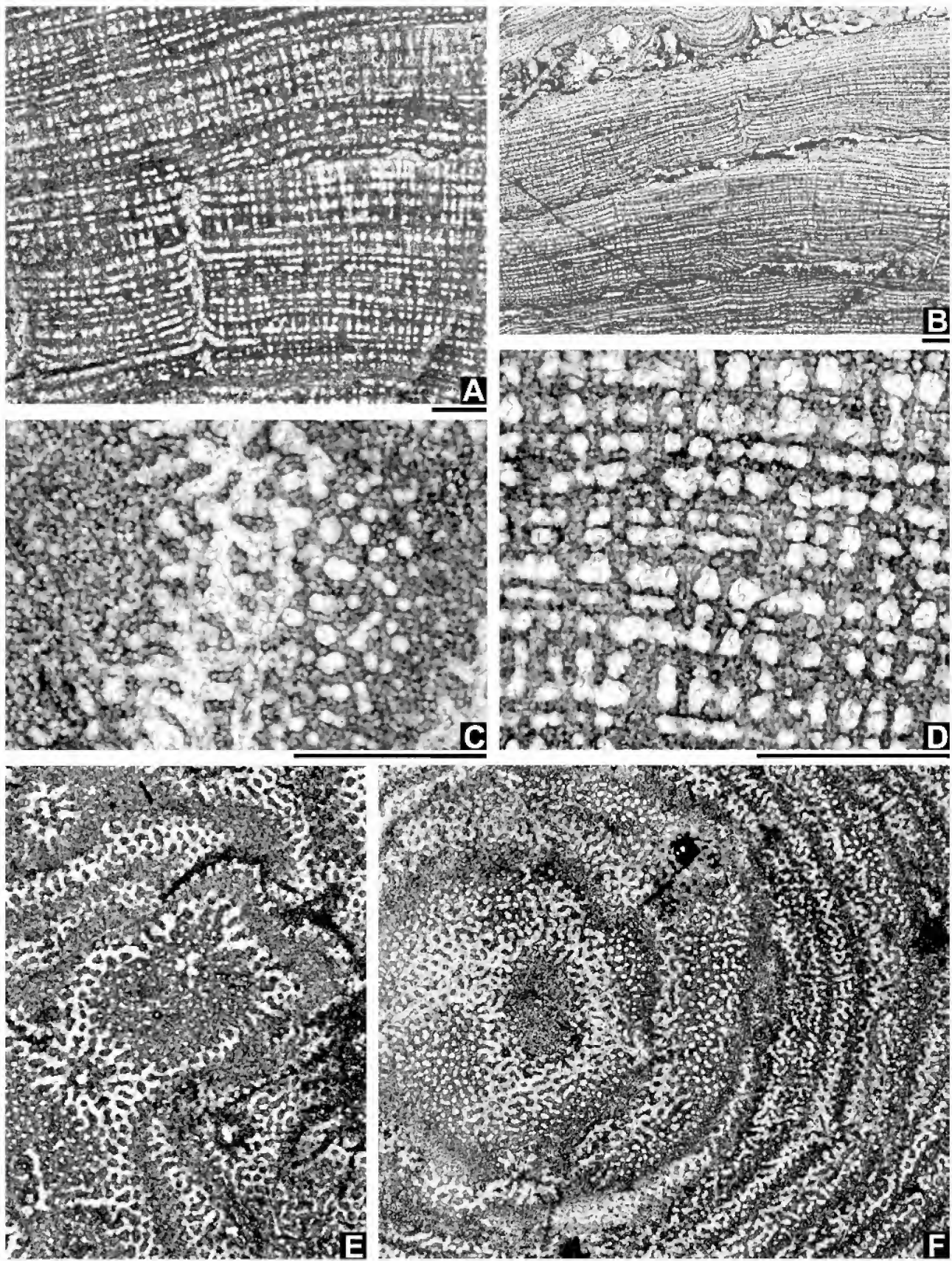


Fig. 3. *Atopostroma distans* (Ripper, 1937): A, C, D, F, from Lomandra Limestone in SD170 section (210 m above the base); (A) longitudinal section, AM F.134879 (AM FT.15066), $\times 10$; (B) longitudinal section, UQF.47741B from locality UQL.2980 of Mallett (1968), from Dip Creek Limestone, 1 km SW of Martins Well, $\times 5$; (C) tangential section, AM F.134879 (AM FT.15067), showing enlarged small area (centre left in Fig. 3F), with irregularly shaped pachysteles in open, spar-filled, interlaminar, ... [continued on facing page]

microreticular features of pachysteles and pachystromes are also largely acosmoreticular in longitudinal section, except clinoreticular where pachysteles margins diverge upwards; sometimes microreticular features masked by diagenetic alteration, leaving skeletal elements preserved predominantly with melanospheric to compact microstructures.

Discussion. Yang & Dong's (1979, p. 74) original generic diagnosis included: laminae thin, compact, without thickened material; pillars thick, upward spreading, superposed across a few laminae, with connecting radial processes; astrorhizae rudimentary; no "pseudozooidal" tubes [=allotubes]; microstructure cellular or maculate. The maculae were apparently darker spheres on a lighter background (equivalent to the melanospheres of Stearn, 1965, 1966). Though resembling *Actinostroma* (given the recognition of hexactinellid type "connecting processes" of actinostromatids), Yang & Dong preferred to group *Atopostroma* as belonging to family Stromatoporidae, and this position was maintained by Dong & Wang (1982) and Wang (1988) in subsequent descriptions of Chinese species. Stearn (1980, 1983) on the other hand favoured a grouping of *Atopostroma* within the Clathrodictyidae because of the characteristic spread of thick, superposed, pillars beneath successive, thin, single-layered laminae (or microlaminae), which suggested a close relationship with clathrodictyid genus *Gerronostroma*. Also, Stearn (1966, p. 101) suggested *Actinostroma stellulatum distans* Ripper, 1937 as a species of *Gerronostroma* (see further discussion below). Mistiaen (1985) however argued that the microstructure in *Gerronostroma* was not the same, and preferred a separate grouping for *Atopostroma*.

Later, Stearn (1990) identified a clinoreticular microstructure in "pillars" of a form he called *Atopostroma tuntouense* from Stuart Bay, Bathurst Island, in Arctic Canada, but not identical with the type species—see Webby *et al.* (1993, p. 173). Additionally, Stearn (1993) reassigned *Atopostroma* to the family Syringostromatidae based on the presence of a microreticular microstructure within the order Syringostromatida. Webby & Zhen (1993) and Webby *et al.* (1993) then followed Stearn's lead, reinterpreting the taxon *Actinostroma stellulatum distans* Ripper, 1937, as another valid representative of genus *Atopostroma*. Others—see Prosh & Stearn (1996), Stearn, *in Stearn et al.* (1999), and May (1999, 2005)—have maintained the grouping of *Atopostroma* within the family Syringostromatidae (order Syringostromatida). As mentioned earlier, Stearn (1993) also commented on the two genera exhibiting transitional forms in the late Lochkovian Martins Well Limestone Member of north Queensland.

Dong (2001, p. 150), after presenting a similar generic diagnosis of *Atopostroma* to the original diagnosis of Yang & Dong (1979, p. 74), adopted a different approach to classifying the genus. Instead of the earlier Yang & Dong assignment to the "stromatoporids", Dong (2001), perhaps,

after giving greater weight to the presence of long pillars and "connecting rods" forming hexactinellid networks, placed *Atopostroma* in the order Actinostromatida, though his conception of the order remained markedly different from groupings adopted by others (see, for example, Stock, *in Stearn et al.*, 1999). Dong (2001) included the genus *Atopostroma* in the family Gerronostromatidae Bogoyavlenskaya, 1969 along with five other genera, and he also transferred that family to the order Actinostromatida. The genera he included altogether in the family were of mixed affinities—clathrodictyid (*Gerronostroma*, *Pseudoactinodictyon*, *Clathrostroma*), stromatoporellid (*Amnestostroma*), syringostromatid (*Atopostroma*) and problematical (*Pseudostromatopora*)—and none of them, with the possible exception of *Atopostroma*, displays features of the Actinostromatida (see Stock, *in Stearn et al.*, 1999 p. 32). Only *Atopostroma* with its microreticulate microstructure could possibly be interpreted as an actinostromatid (but here it is preferentially treated as a part of the order Syringostromatida). Only approximately half of Dong's (2001) listed genera belong to the family Gerronostromatidae, and that family, according to Nestor (*in Stearn et al.*, 1999, p. 23), belongs to the order Clathrodictyida. All the families of the Clathrodictyida developed a compact skeletal microstructure.

The genus *Atopostroma* has proven to exhibit an original microreticular microstructure, and it only apparently produces a compact or melanospheric (= Dong's "maculae") microstructure when affected by secondary diagenetic processes. Here, we treat the primary skeletal microreticulation as having a primary focus in the classification of genus *Atopostroma*, and therefore the genus is as an indubitable member of the order Syringostromatida. It may have a link to actinostromatids given that some taxa exhibit small-scale structures such as micropillars and microcolliculi, like the genus *Densastroma* Flügel, 1959 (e.g., within the family Densastromatidae Bogoyavlenskaya, 1974), but it is not closely related to a genus like *Actinostroma* that has long pillars with a compact microstructure, as suggested by Dong (2001).

Species of *Atopostroma* are widely distributed in Devonian sequences worldwide: in particular they are reported from the Lower Devonian (Lochkovian) of Arctic Canada and New York, USA (Stearn, 1990; Stock, 1997); in the Lower Devonian (Pragian) of Bohemia, Czech Republic (Počta, 1894; May, 1999, 2005); in the Lower Devonian (Pragian-Emsian) of eastern Australia (Ripper, 1937; Webby & Zhen, 1993, Webby *et al.*, 1993; and herein); Lower Devonian (Emsian) of Arctic Canada and Yukon (Stearn, 1983; Prosh & Stearn, 1996), and from Guangxi and Sichuan in China (Yang & Dong, 1979; Dong, 2001); as well as from the Middle Devonian of the Kuznetsk Basin, Russia (Yavorsky, 1955), Yunnan, in China (Dong, 2001) and possibly from Afghanistan (Mistiaen, 1985).

[Fig. 3 continued] ... gallery space that grades up into an area defined by a mix of interconnected microreticulate material between small, enclosed spar-filled galleries, and darker, denser, pachystromal layers with a more uniform microreticulation of differentiated micropillars that interconnect to microcolliculi around tiny microgallery spaces towards top, x35; (D) longitudinal section, AM F.134879 (AM FT.15066), showing a acosmoreticular to clinoreticular microstructure, upwardly expanded to hour-glass shaped, superposed pachysteles, and a somewhat irregularly thickened pachystromal layer of microlaminae with the uppermost microlamina usually having the greatest continuity, x35; (E) tangential section, AM F.134882 (AM FT.15073) from the Lomandra Limestone of SD170 section, 274m above the base, x10; F, tangential section, AM F.134879 (AM FT.15067), x10—for detail see Fig. 3C. All scale bars = 1 mm.

Atopostroma distans (Ripper, 1937)

Fig. 3A–F

Not *Actinostroma frustulum* Počta, 1894:145, pl. 18 bis, figs 1–4.–E. Flügel & Flügel-Kahler, 1968:168 (*cum syn.*).–May, 1999:176.–May, 2005:210, 212, 248 (table 26); pl. 25, figs 1a,b, 2a,b; pl. 34 fig. 1a,b, pl. 35, fig. 1; pl. 41, fig. 2a,b.

Actinostroma stellulatum var. *distans* Ripper, 1937:12, pl. 2, figs 1–2.–Ripper, 1938:223, 236, 240.–Teichert & Talent, 1958:16.

?*Actinostroma* cf. *distans* Ripper.–E. Flügel, 1958:180.–H. Flügel, 1961:47.

Actinostroma (*Actinostroma*) *distans* Ripper.–E. Flügel, 1959:142.

Actinostroma stellulatum distans Ripper.–E. Flügel & Flügel-Kahler, 1968:403.

Trupetostroma cf. *ideale* Birkhead.–Stearn & Mehotra, 1970:16, pl. 5, figs 1,2.

Part *Nexilamina dipcreekensis* Mallett, 1971:244, pl. 14, fig. 4 only.

Atopostroma tuntouense Yang & Dong.–Stearn 1983:548, fig. 4E–H.

Not *Atopostroma tuntouense* Yang & Dong.–Stearn, 1990:496, figs 4.1, 4.2, 8.2.

Atopostroma distans (Ripper).–Webby & Zhen, 1993:346, figs 11A–D, 12E.–Webby, Stearn & Zhen, 1993:171, figs 27F, 28A–D.–Prosh & Stearn, 1996:36, pl. 18 fig. 5.

Material. Four specimens, including SD170-210-1 (AM F.134879, AM FT.15066, AM FT.15067), SD170-217-1 (AM F.134880, AM FT.15068, AM FT.15069), SD170-270-3 (AM F.134881, AM FT.15070, AM FT.15071) and SD170-274-3 (AM F.134882, AM FT.15072, AM FT.15073), from 210 m, 217 m, 270 m and 274 m, respectively, above base of Lomandra Limestone (upper Emsian), SD170 section of Mawson *et al.* (1988) in Lomandra Creek type section; and other specimens from C.W. Mallett's collection as follows: UQF.47741, from UQL.2980, 500 m above base of section, Martins Well (MW) traverse, 1 km SW of Martins Well (Mallett, 1971) and UQF.47750, from UQL.2981, 800 m above base of section of MW traverse of Mallett (1971), both from Dip Creek Limestone—note the former specimen was erroneously included in description of *Nexilamina dipcreekensis* by Mallett (1971, p. 244, pl. 14, fig. 4); UQF.47600, from UQL.2974—collected from loose rubble, probably derived from the Chinaman Creek Limestone at South Chinaman Creek, 5 km N of the abandoned Pandanus Creek homestead; two other specimens, respectively, UQF.48243 from UQL.2698, and UQF.48142 apparently comes from the same locality, 2.5 km SSE of Pandanus homestead, with one (UQF.48142) a reworked sample (it came from “isolated rudites” (Mallett, 1971, p. 243), now assigned to the Late Devonian Bulgeri Formation (Lang, 1993); consequently, the other (UQF.48243) is also a reworked specimen.

Description. Skeleton domical, with width and height up to 140 mm; growth surfaces smooth to slightly wavy, but only to extent of forming weak mamelons; growth interruptions define a few, 1 to 3 mm thick, latilaminae, though one specimen (UQF.47741) from the Dip Creek Limestone, SW of Martins Well, has conspicuous latilaminae, 4 to 5 mm thick (Fig. 3B). Astrorhizae moderately well developed, with

centres near tops of mamelons or offset to sides, spaced much closer, 2.5 to 4.5 mm apart, in Broken River material (Fig. 3E), as compared with the holotype (NMV P141754-57, ex MUGD) from the Buchan Caves Limestone of eastern Victoria, with its centres spaced 7 to 9 mm apart; each localized centre has a stellate, outwardly radiating, cluster of up to 12 canals; usually canals are from 0.10 to 0.18 mm wide, and extend laterally within an interlamina space for a millimetre or more; canals of each cluster are deflected sharply upwards into single, radially aligned, 0.2 to 0.3 mm wide, tabulated, astrorhizal passageway that leads towards growth surface (Fig. 3A).

In longitudinal section pachysteles (pillars where poorly preserved) superposed continuously through many laminae (up to 25 counted) though in a few places continuity much more limited, even locally absent or restricted to only one or two interlamina spaces; commonly spreading upward, but sometimes more spool- or post-shaped, spaced from 9 to 12 in 2 mm laterally; usually range from 0.08 to 0.20 mm in diameter, but may become more expanded outwardly and upwardly towards top. Pachystromes (or laminae where microreticulation not clearly visible), continuous, of variable thickness (0.05 to 0.18 mm thick), and with spacing from 8 to 12 in 2 mm; sometimes clearly defined by microlaminae at top, from 0.020 to 0.025 mm thick (though in extremes to 0.05 mm thick), and one or two, discontinuous, slightly disordered, rows of microlaminae below, each pair intersected by set of short, pachysteles-derived micropillars to form microgalleries, from 0.03 to 0.05 mm in width; in places tiny, darker, melanospheric specks, about 0.01 to 0.02 mm in diameter, visible along microlamina within more-or-less continuous dark line, or may be identified at intersections of microlaminae and micropillars; additionally, in well preserved specimen (SD170-210-1 – AM F.134879), in areas where spool-shaped pachysteles are intersected, rather disordered and disrupted row of microgalleries may develop above a microlamina (Fig. 3D); more commonly, however, skeletal material is less well preserved, with fine structures showing a more diffused compact microstructure, though ghosts of microreticulation may be preserved in form of scattered, vaguely aligned, rows of tiny melanospheric specks. Spar-filled gallery spaces prominent, commonly dome-shaped to vertically ovate or rounded; in some places subdivided by small, low convexity, dissepiments; rarely, longer, wavy, microlamina-like dissepiments occur, and these may act as local pachystromal floors; occasionally pores, about 0.05 mm wide, seen to disrupt continuity of bounding microlaminae. In pachystromal areas microstructure has characteristics of acosmoreticular, whereas in pachysteles microreticulation is irregular, somewhat disordered and slightly divergent, with larger microgalleries reaching 0.05 to 0.07 mm in width; hence these areas include a mix of acosmoreticular and clinoreticular patterns.

In tangential section skeletal framework of pachysteles and pachystromes shows broad differentiation of structural and microreticular elements between successive “interlamina” layers, broadly divided into three parts (Fig. 3C): near the base the pachysteles appear as rounded to oval, occasionally more elongated to vermiform shapes within extensive, “open”, gallery spaces (and astrorhizae); pachysteles have microreticulate (?acosmoreticular) interiors of subspherical microgalleries, up to 0.04 mm in diameter, and bounded by rod-like microcolliculi and intersected by micropillars;

where pachystele margins are incomplete, the ends of microcolliculi may be frayed; in middle part, pachyστελεs are more anastomosing to coalesced, with rounded to oval to irregular spar-filled gallery spaces, usually ranging from 0.06 to 0.15 mm in diameter; and inside pachystele walls is well developed acosmoreticular network of microgalleries, from 0.03 to 0.05 mm across; in upper part where pachystromal elements and microlaminae are intersected the microreticulate networks of microgalleries are darker and denser and on average about 0.03 mm in diameter; in small areas where beam-like microcolliculi are not intersected the microgalleries are incomplete or show only aligned rows of tiny rounded micropillars, 0.01 to 0.02 mm in diameter (or sometimes they appear to be preserved as similar-sized melanospheric specks); also in a few places microgalleries arranged in gently meandering patterns, appearing like wall-less microcanals, 0.02 to 0.03 mm wide, and traceable for distances of about 0.4 mm in length (Fig. 3C); the patterns of pachystromal elements with differentiated microlaminae maintain a finely porous, microreticulation, unless skeletons suffer significant diagenetic alteration that seems to cause production of more continuous sheet-like microlaminae.

Remarks. The preservation of one specimen (SD170-210-1 – AM F.134879, see Fig. 3A, C, D, F) of *Atopostroma distans* (Ripper, 1937) from the Lomandra Limestone of the Broken River area is exceptional in exhibiting so much microstructural detail. Described material from all other localities in Australia and elsewhere shows much less well preserved specimens. A close comparison of the holotype and some topotypes of *A. distans* from the Buchan Limestone at Heath's Quarry in Victoria (Ripper, 1937; Webby *et al.*, 1993), has been made recently, in an attempt to reveal more detail about the microstructure. Unfortunately most of this material shows melanospheric, compact, and/or fibrous microstructures, all of which would appear to have developed from secondarily, diagenetic alteration of its original microreticular skeletal elements. Tangential sections of the types were first mentioned by Ripper (1937, p. 13) as having “an appearance which seems to anticipate the porous structure of *Stromatopora* and allied genera”, and Webby *et al.* (1993, p. 171) who reported “cellules” in structural elements of lower, less dense, parts of interlaminar spaces (see also Webby & Zhen, 1993, fig. 12E). The Victorian material in further detailed study shows little direct evidence in both longitudinal and tangential sections of having an original microreticulate skeleton. A number of specimens show discontinuous, single rows of microgalleries between pairs of microlaminae (including the topmost microlamina) and pachyστελεs (rather than pillars) are identified with disordered (acosmoreticular) and vaguely perpendicular-to-growth microstructures in longitudinal sections of three specimens, including the holotype. Tangential sections of the holotype and another specimen show rounded, to elongate or irregular pachystele outlines with well-defined clusters of microgalleries in their interiors and frayed margins that represent the cut ends of rod-like microcolliculi. These microreticulate structures can all be closely matched with the *A. distans* material studied in the Broken River region. The Victorian types also show matching arrangements of melanospheric dots—patterns such as microlaminae exhibiting a single, discontinuous, parallel-to-growth, row

of melanospheric specks (0.015 to 0.025 mm apart), and less common perpendicular-to-growth rows of dots within pachyστελεs (or pillars).

The New South Wales Jesse Limestone material of *A. distans* is morphologically similar to the Victorian type and other material, and apparently comes from limestones of more-or-less equivalent, early Emsian age (Webby & Zhen, 1993). Though the specimens come from widely separated localities in south-eastern Australia they exhibit surprisingly few skeletal or preservational differences. Just a few minor differences seemingly exist between them. For example, scattered, small, long-low to more upwardly convex cyst-like dissepiments occur close to bases of “interlaminar” spaces in specimens from both localities; only one significant difference is noted in some Jesse material, particularly one, specimen AM F. 85595 (formerly listed as Sydney University Palaeontology no. SUP97230), that has developed localized, wavy, microlamina-like dissepiments within wider than normal interlaminar spaces (see Webby & Zhen, 1993, fig. 11A). A few Jesse specimens are seemingly less well-preserved, showing a fibrosity that seems to more-or-less mimic traces of an original skeletal microreticulation, shown elsewhere in the same specimens as rows of lighter subspherical voids that possibly represent traces of the original microgalleries.

May (1999, 2005) in a revision of the Devonian stromatoporoids from Bohemia, Czech Republic, designated lectotypes of a number of species, including *Actinostroma frustulum* Počta, 1894 from the Koněprusy Limestone (middle Pragian) near Koněprusy (“hill near Plesivec”). Study of the lectotype of *A. frustulum* and 12 new specimens from western and eastern quarries near Koněprusy (respectively, “Čertovy schody-Zapad” and “Čertovy schody-Vychod”; see May 2002, fig. 1) allowed May (1999, p. 168) to identify the species as having a microreticulate (clinoreticular) microstructure and consequently interpreted *A. frustulum* as a species of the genus *Atopostroma*. Furthermore, on the basis of inferred morphological similarities, May (1999, 2005) proposed *A. distans* (Ripper, 1937) as a junior synonym of *A. frustulum* (Počta, 1894). Stearn (2001, p. 14) initially questioned this interpretation on the basis that the Czech material had not been adequately illustrated but a much more complete documentation (and illustration) of the species has since been made by May (2005). The fuller description and illustrations allow the relationships between the two species to be clarified, and to determine that *A. frustulum* has a markedly different microreticulation. May (1999, 2005, p. 210) recorded a finer clinoreticular network, with microgalleries about 0.015 mm across in *A. frustulum*, whereas the dominant microreticulation in *A. distans* is acosmoreticular, though also clinoreticular in areas where pachyστελεs expand upwards. In the type material from Victoria (Webby *et al.*, 1993, p. 171) the microgalleries, though previously recorded as ranging from 0.01 to 0.03 mm in diameter, based on a recent reexamination of this material, are far more variable, from 0.01 to 0.05 mm (most commonly 0.03 to 0.04 mm) in diameter.

The second difference is that pachyστελεs based on the lectotype of *A. frustulum* (see May 2005, pl. 41 fig. 2b) are more slender than is characteristic of *A. distans*. Another example of *A. frustulum* is illustrated by May (2005, pl. 25 fig. 1b) is more comparable but it is not a type specimen. Yet another specimen labelled as *A. frustulum* (illustrated

in tangential section by May (2005, pl. 25 fig. 2b) shows pachysteles that are markedly broader than those exhibited by *A. distans*; indeed this specimen seems to be more closely related to the second described species of *Atopostroma* from Bohemia, *A. contextum* (Počta, 1894)—see May 2005, p. 206, pl. 41 fig. 1b). Consequently, *A. distans* remains a valid and independent species—with its more coarsely acosmoreticular and locally clinoreticular microstructure than the exclusively finely clinoreticular patterns of *A. frustulum* and *A. contextum*, and with its pachysteles that are typically thicker than those of *A. frustulum*, and thinner than those of *A. contextum*.

The better preserved skeletal material of *A. distans* from the Broken River area of Queensland has a typical microreticulation within both pachysteles and pachystromes. The pachystromes are not easy to characterize but intergrade with adjacent pachysteles and may be associated also with sets of closely spaced microlaminae especially towards upper surfaces. It seems that no clear-cut determination of a specific type of microreticulate microstructure (Stock, 1989) can be made for this well preserved species of *A. distans*. All the basic microreticulated structures of the skeleton seem to be acosmoreticular, except where pachysteles diverge upwards and in lower parts of spool-shaped pachysteles where the microreticulation locally converges upward, the condition is clinoreticular, (Fig. 3C).

Atopostroma stearni n.sp.

Fig. 4A–F

Not *Atopostroma tuntouense* Yang & Dong, 1979:74 pl. 41, figs 7, 8.

?*Atopostroma tuntouense* Yang & Dong.—Stearn, 1990:496, figs 4.1, 4.2, 8.2.

Material. Five specimens, including holotype MW6-8 (AM F.134883, AM FT.15074, AM FT. 15075, AM FT.15076) and four paratypes MW1-5 (AM F.134884, AM FT.15077, AM FT.15078 – paratype A), MW20-3 (AM F.134885, AM FT.15079, AM FT.15080 – paratype B), MW20-4 (AM F.134886, AM FT.15081, AM FT.15082, AM FT.15083—paratype C), and MW35-8 (AM F.134887, AM FT.15084, AM FT.15085, AM FT.15086—paratype D), are from the Martins Well Limestone Member of the Shield Creek Formation (late Lochkovian-early Pragian) in the MW section of Mawson *et al.* (1988) near Martins Well; holotype from 6 m above base of MW section, and paratypes, respectively, from 1, 20 and 35 m above base of section, and two additional paratypes, JAL-T/4 (AM F.134888, AM FT.15087, AM FT.15088—paratype F) and JAL-T/6 (AM F.134889, AM FT.15089, AM FT.15090—paratype E), from the upper limestone member of the Jack Formation (earliest Lochkovian) of the Broken River Gorge section are referred to the species. Two less well preserved specimens, JAL-T/3 (AM F.134890, AM FT.15091, AM FT.15092) and JAL-T/17

(AM F.134891, AM FT.15093, AM FT.15094), are from the same horizon and locality.

Derivation of name. After Colin W. Stearn, who has contributed so much to contemporary understanding of Palaeozoic stromatoporoids in general, and to orders Stromatoporoida and Syringostromatida, including the genus *Atopostroma*, in particular.

Diagnosis. Species of *Atopostroma* with pachysteles typically exhibiting upwardly expanding to irregularly post-shaped, and commonly superposed through up to 20 successive pachystromal layers; each pachystrome has a capping of an extended, rather even thin microlamina at top and unevenly suspended microreticular network of pachystrome and associated pachysteles elements below; pachystromes variably spaced, about 12 to 17 in 2 mm but usually exhibits two distinctly different successional spacing arrangements, with closely clustered microlaminae, and more widely spaced pachystromal elements, and between these there are elongated, wavy, microlamina-like dissepiments that in places act as raised pachysteles floors; microstructure largely acosmoreticular.

Description. Skeleton domical to laminar with dimensions up to 160 mm in height and 260 mm diameter. Growth surfaces smooth, flattened to gently undulating except for a few small, locally upraised, mamelons up to 1 mm high, at least 0.6 mm wide (Fig. 4A); astrophorae most conspicuous in tangential sections, with centres spaced from 3 to 7 mm apart, and including 5 to 8 main, non-tabulated, radiating branches, from 0.10 to 0.20 mm wide (Fig. 4B); most commonly astrorhizal canals located in lower interlaminar spaces but characteristically upturn in places into single, tabulated, longitudinally-orientated, canals that interconnect with astrorhizal centres; sometimes canals are with mamelons. Latilaminae defined by growth interruptions and phase changes, from 1 to 6 mm thick; in one part of holotype an extensive layer of disordered microreticular, dissepiment and canal-like skeletal material, up to 1 mm thick, has developed between successive latilaminae (Fig. 4A, 4E); this layer may represent a kind of basal phase to growth of overlying latilamina.

In longitudinal section skeletal structures dominated by long, thin, even, laterally persistent, microlaminae at tops of pachystromes, and irregularly upward-spreading pachysteles below, these latter commonly superposed but not usually through more than about 12 to maximum of 20 successive “interlaminar” spaces (Fig. 4A, 4D); the single, mainly continuous, microlaminae usually appear as dark, rather dense, plates, about 0.02 mm thick; only rare breaks in continuity occur, that suggest presence of occasional, scattered, small pores, with diameters of 0.02 mm (and perhaps related to original microreticulation). Skeletons show spacing of pachystromes varying widely; on average measurements range from 12 to 17 in 2 mm, though

Fig. 4 [continued from facing page] ... (D) longitudinal section (AM FT.15074), showing characteristic mix of close-spaced pachystromal microlaminae, and more wider spaced microlaminae enclosing the mainly microreticulated superposed, upward-flaring pachysteles, $\times 35$; (E) longitudinal section (AM FT.15074), showing detail of successive growth interruptions and intervening phase of more disorderly arrangement of dissepiments, canal-like tubes and microreticular material, $\times 25$; (F) tangential section (AM FT.15075), showing a well-developed acosmoreticular skeletal network associated with pachysteles, and in denser pachystromal layers including the discrete microlaminae, $\times 35$. All scale bars = 1 mm.

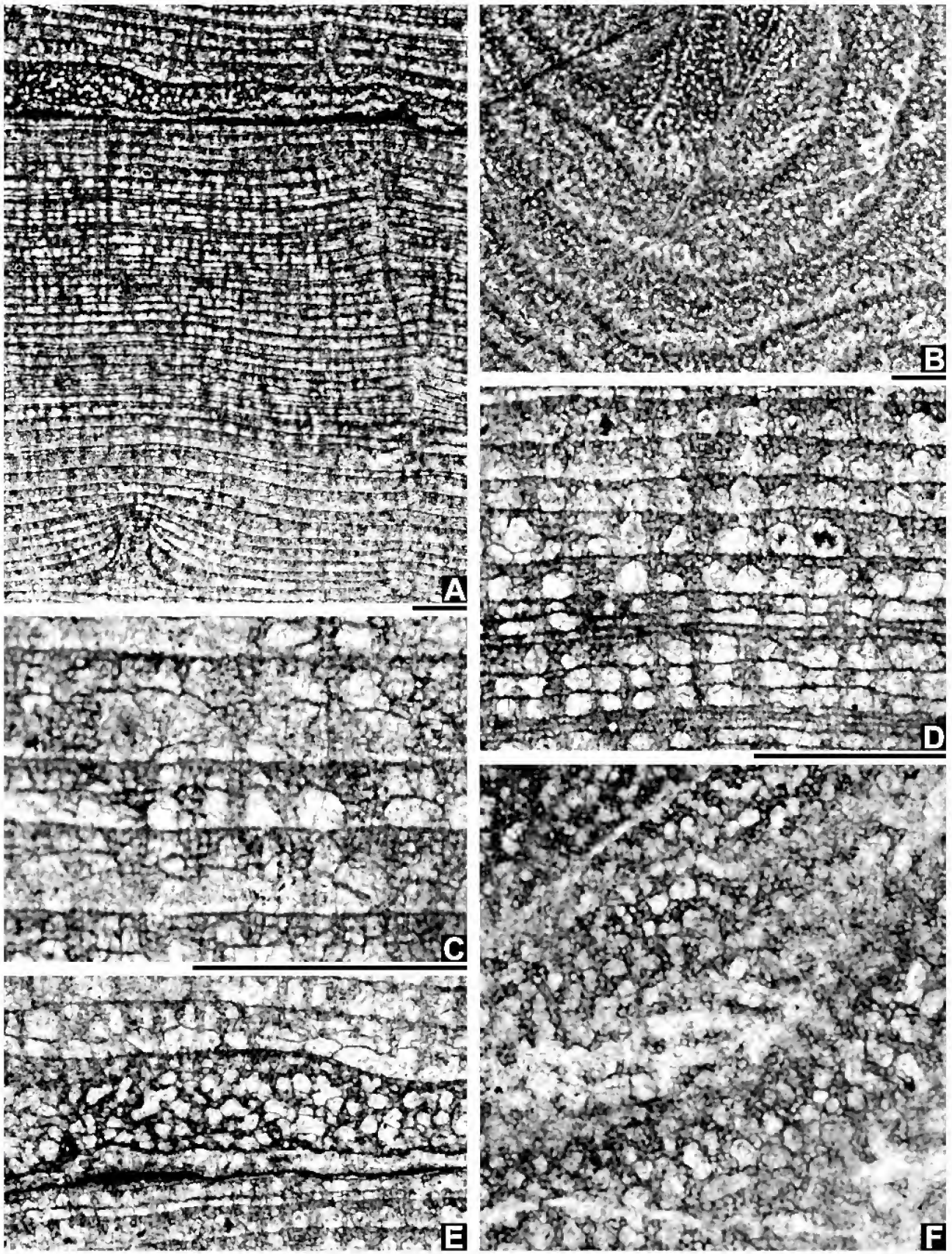


Fig. 4. *Atopostroma stearni* n.sp., A–F, holotype AM F.134883 from Martins Well Limestone Member (Shield Creek Formation), 6 m above the base of the MW section; (A) longitudinal section (AM FT.15074), showing latilaminae with phase changes and a distinctive mamelon, $\times 10$; B, tangential section (AM FT.15075), $\times 10$; (C) longitudinal section (AM FT.15074), showing incomplete microlamina-like dissepiments that intersect interlaminar areas between widely spaced, regular, microlaminae, $\times 50$; ... [continued on facing page]

successively sets of microlaminae are either wide spaced or narrowly spaced; where microlaminae are widely spaced (e.g., 0.15 to 0.35 mm apart), individual “interlaminar” spaces are divisible broadly into two parts, a lower, occupied by gallery spaces, astrorhizae and narrower, ends of the pachyestes, and an upper part represented substantially by spread of pachyeste and pachystrome-derived microreticular material that even extends around tops of associated gallery spaces; wavy microlamina-like dissepiments may locally intervene between lower and upper parts, and where present may provide raised floors for development of pachyestes, and may subdivide larger spar-filled galleries into two (Fig. 4C,D). Pachyestes typically expand upwards, from 0.03 to 0.10 mm wide in lower part, to 0.15 mm, even to 0.2 mm wide towards top; and a spacing from 9 to 10 in 2 mm laterally; skeletal material is predominantly acosmoreticular, though at margins of some pachyestes, patterns may be vaguely clinoreticular. Where narrowly spaced, the laterally persistent subparallel to parallel microlaminae occur in sets of two, three or more (Fig. 4D); spaces between microlaminae may be partially occupied by microgalleries containing microcolliculated microlaminae and short micropillars (from 0.02 to 0.04 across), or micropillars are absent or incomplete, appearing as a row of ?melanospheric dots along a microlamina, about 0.01 mm wide; or these structures may develop a vaguely radial fibrosity possibly where poorly preserved. In addition to undulating microlamina-like dissepiments some small, blister-like dissepiments may be scattered in places within skeleton; they mainly subdivide galleries, especially in lower parts of “interlaminar” spaces; spar-filled galleries characteristically dome-shaped, from 0.10 to 0.20 mm across.

In tangential section, pachyestes rounded to elongated, or irregular, from 0.05 to 0.15 (rarely to 0.20) mm in diameter in “open” gallery areas of lower part of “interlaminar” space; usually pachyestes have frayed margins as result of rod-like, microcolliculli being intersected; pachyestes spread outwards to develop more completely anastomosing network across middle part of “interlaminar” space, including completely enclosed, spar-filled galleries, typically 0.10 to 0.15 mm in diameter (Fig. 4F); microreticular elements acosmoreticular, with microgalleries from 0.025 to 0.050 mm across, and orderly rounded micropillars (0.010 to 0.015 mm across) where microcolliculi intersected. In upper part of “interlaminar” space more uniformly, denser and darker band-like areas (Fig. 4B), that mainly represent parts of obliquely intersected microlaminae near tops of “interlaminar” spaces; finely porous, microreticular network of microgalleries, which are 0.02 mm across (on average); rounded micropillars where they can be differentiated are about 0.01 mm in diameter.

Remarks. The type species, *A. tuntouense* Yang & Dong, 1979, from the Yujiang Formation (Emsian) of South China bears a resemblance to *A. stearni* but its pachyestes are thicker, consequently more widely spaced (6 to 8 in 2 mm), and more regularly superposed, and it lacks any significant development of dissepiments. Material from the Lower Devonian (upper Lochkovian) Stuart Bay Formation of Arctic Canada was first described as *A. tuntouense* by Stearn

(1990, p. 496), but has since been recognized as belonging to a different species from the type species (see Webby *et al.*, 1993) having, for example, a much closer spacing of laminae (16 in 2 mm). This Stuart Bay species, now assigned by Stearn (in press), and illustrated in the *Treatise* volume as “*Atopostroma* n.sp. = *A. tuntouense* of Stearn, 1990, p. 496”, bears close relationships to the late Lochkovian/early Pragian *A. stearni* of the Martins Well Limestone Member in northern Queensland. However though it has a similarity in the spacing of laminae (or pachyestromes), the Stuart Bay form shows certain differences that may be of taxonomic importance. Firstly it is described as exhibiting a clinoreticular microstructure, whereas *A. stearni* is dominantly acosmoreticular. Secondly, though it is recorded as having “broadly undulate” microlaminae where they are locally close spaced, the Stuart Bay form does not apparently exhibit the association of more widely spaced microlaminae and intervening wavy microlamina-like dissepiments. Consequently, the Canadian form is only doubtfully regarded as conspecific with *A. stearni*.

Atopostroma stearni also bears close resemblances to *A. distans* (Ripper, 1937) from the Early Devonian (Emsian) successions of Victoria (Webby *et al.*, 1993), central New South Wales (Webby & Zhen, 1993), and North Queensland (herein), but differs mainly in having on average more closely spaced pachyestromes (or laminae), from 12 to 17 in 2 mm, compared with spacing of pachyestromes (or laminae), from 7 to 11 in 2 mm in *A. distans*, and *A. stearni* more commonly exhibits dissepiments both long, wavy microlamina-like and small cyst-like types. Also, in *A. distans*, pachyestes may be spool-shaped with the microreticulation, not only typically diverging upwards, but also, locally, converging in the lower parts of pachyestes, a feature not seen in *A. stearni*, and the pachyestes are more markedly superposed in *A. distans* than in *A. stearni*.

Atopostroma sp. 1 from the Dayville Member of the Coeymans Formation (Lochkovian) in New York (Stock, 1997) is another possibly related form, though its pachyestes are slightly thicker than in *A. stearni*, and no long, wavy, dissepiments occur; consequently Stock’s *Atopostroma* sp. 1 is not conspecific with *A. stearni*. A second species recorded by Stock (1997) as *Atopostroma* sp. 2 from Deansboro Member of the Coeymans Formation is likely to belong to another syringostromatid genus, possibly *Coenostroma* Winchell, 1867.

Somewhat transitional relationships exist between species of *Atopostroma* such as *A. stearni*, and species of *Habrostroma*, not only in the Martins Well Limestone Member. For example, the microreticulation is similar, that is, mainly acosmoreticular, in both genera *Atopostroma* (herein), and *Habrostroma* (Stock, 1991, p. 903). Secondly, the pachyestes of *A. stearni* are less continuous and regularly superposed than in some other species of *Atopostroma*, whereas though typically species of *Habrostroma* have short pachyestes, some do have superposed pachyestes not unlike *A. stearni*. For example, the Lochkovian species *Habrostroma microporum* and *H. centrotum* (see Stock, 1991, 1997, figs 4–7) exhibit superposed pachyestes, and like *A. stearni* commonly exhibit long, wavy, microlamina-like dissepiments.

Atopostroma protentum n.sp.

Fig. 5A–G

Material. Eleven specimens, including holotype MW1-1 (AM F.134892, AM FT.15095, AM FT.15096), and ten paratypes MW1-20 (AM F.134893, AM FT.15097, AM FT.15098—paratype A), MW6-4 (AM F.134894, AM FT.15099, AM FT.15100—paratype B), MW6-6 (AM F.134895, AM FT.15101, AM FT.15102—paratype C), MW6-7 (AM F.134896, AM FT.15103, AM FT.15104—paratype D), MW6-9 (AM F.134897, AM FT.15105, AM FT.15106—paratype E), MW6-10 (AM F.134898, AM FT.15107, AM FT.15108, AM FT.15109—paratype F), MW6-11 (AM F.134899, AM FT.15110, AM FT.15111—paratype G), MW6-12 (AM F.134900, AM FT.15112, AM FT.15113—paratype H), MW6-13 (AM F.134901, AM FT.15114, AM FT.15115—paratype I) and MW6-20 (AM F.134902, AM FT.15116, AM FT.15117—paratype J), from the Martins Well Limestone Member, Shield Creek Formation of the MW section of Mawson *et al.* (1988) near Martins Well; holotype from 1 m above base of MW section, and paratypes, respectively, from 1, 6, and 20 m above base of section. Two other specimens, MW1-18 (AM F.134903, AM FT.15118, AM FT.15119), and MW35-9 (AM F.134904, AM FT.15120, AM FT.15121) are included in the species, and doubtfully, MW1-9 (AM F.134905, AM FT.15122, AM FT.15123), MW1-17 (AM F.134906, AM FT.15124, AM FT.15125) and MW6-18 (AM F.134907, AM FT.15126, AM FT.15127); these all come from the same horizon and locality as the type material, respectively, from 1 m, 6 m and 35 m above base of section. Three of the specimens [MW6-6 and MW6-7 (AM F.134896—paratype C, and AM F.124896—paratype D), and specimen MW1-18 (AM F.134903)] are intergrown with an unnamed cyanobacterium.

Derivation of name: Latin, *protentum*, stretched out, lengthened—alluding to the dominantly wide-spaced microlaminae.

Diagnosis. Species of *Atopostroma* with pachysteles typically exhibiting upwardly expanding to irregular, even locally, spool to post-like, shapes, and may be superposed through up to 12 successive pachystromal layers; each pachystrome has capping of laterally continuous, gently undulating, thin microlamina at top, and unevenly suspended microreticular network beneath, composed of pachystromal and associated pachysteles elements; spacing of pachystromes varies from 5 to 11 (usually 7 to 8) in 2 mm, that is, they are relatively widely spaced, and commonly they have intervening, thin, wavy, microlamina-like dissepiments that act as raised pachysteles floors; microstructure dominantly acosmoreticular.

Description. Skeleton laminar to domical, with maximum height of 110 mm and maximum diameter of 220 mm. Growth surfaces smooth to slightly wavy, rarely showing small mamelons. Latilaminae apparently absent, but a few discontinuity surfaces preserved. Astrorhizae conspicuous in skeletons, especially well shown in tangential sections (Fig. 5B), with individual stellate clusters centred between 4 and 10 mm apart; centres connect to vertical astrorhizal canal, 0.2 mm across; each centre has up to 10 outwardly radiating and branching astrorhizal canals, from 0.1 to 0.2 mm wide; no

tabulae associated. Small, updomed, mamelonate structures, possibly related to astrorhizal system, are 1 mm high and 0.5 mm wide.

Caunopore tubes commonly associated in stromatoporoid skeletons, as intergrown, phaceloid (longitudinally aligned) and tabulated corallites of coral *Syringopora*; corallites vary from 0.3 to 1 mm (usually 0.7 to 0.8 mm) in diameter, and typically show tabulae with infundibuliform floors and/or axial syringes (Fig. 5A,B); also in a few places tabulate coral exhibits lateral branching. Microlaminae of stromatoporoid characteristically downflexed slightly at intersections with caunopore tubes. Small, solitary rugosan, about 1.0 to 1.7 mm in diameter, also intergrown in places, and helicoid spiralling “worm tubes” (*Helicosalpinx*) with diameter of 0.9 to 1.0 mm. In addition, in localized areas of some stromatoporoid skeletons, especially close to, or along, discontinuity surfaces (perhaps associated with intervals of slowing, or cessation, of stromatoporoid growth) an undescribed, problematical, cyanobacterium occurs as upright dendroid growths of dark, thread-like tubules (Fig. 5F) that may be partitioned into “cellules”, 0.02 to 0.035 mm across, to maximum width of 0.05 mm; as well as various parallel-to-growth aspects—where threads may appear like strings of beads and as clusters on surfaces adjacent to, or within individual microlamina; at points of lateral budding a noticeable tendency occurs for chainlike row of “cellules” to increase rapidly in size; colonization by this microorganism is typically within the microreticulate networks of pachysteles and within some porous microlaminae.

Stromatoporoid skeleton exhibits prominent, evenly spaced, laterally continuous, flattened to gently undulating, and relatively thin, microlaminae; most commonly a single, microlamina occurs, but locally in a few places may divide into two, but rarely continues in a closely paired relationship, even laterally may merge into a single microlamina again; in addition localized, thin, compact, undulating, microlamina-like dissepiments occur, but typically these occur towards middle of more widely spaced “interlaminar” spaces (where successive microlaminae are spaced between 0.25 and 0.95 mm apart); these microlamina-like dissepiments have comparatively limited lateral continuity; also smaller, irregular, low convexity and obliquely aligned, dissepiments (like normal cyst plates) may occur, usually in lower part of “interlaminar” space. Microlaminae usually have a variable thickness (0.01 to 0.03 mm thick) and appear to have compact microstructure but some show a mid-line row of tiny, darker (?melanospheric) dots, about 0.035 mm apart, or in other places are vaguely microreticulated; also breaks in continuity of microlaminae occur in places suggesting small pores, 0.02 to 0.025 mm across; a few other pores are larger, to 0.05 mm across; spacing of microlaminae ranges from 5 to 11 in 2 mm (most commonly 7 to 8 in 2 mm).

Pachysteles are from 0.06 to 0.20 mm in diameter near base, and characteristically spread upward and outward, and enclose irregular microreticular network, coalescing against undersurfaces of overlying microlaminae; however, much irregularity exists in pachysteles shapes (Fig. 5G), with some more spool- or post-like, or may be less well developed in certain areas, for example, where microlaminae are close spaced, less than 0.1 or 0.2 mm apart; or where they are more widely spaced, pachysteles may be incompletely developed below middle parts of “interlaminar” space, being replaced by spar-filled areas (galleries, astrorhizal

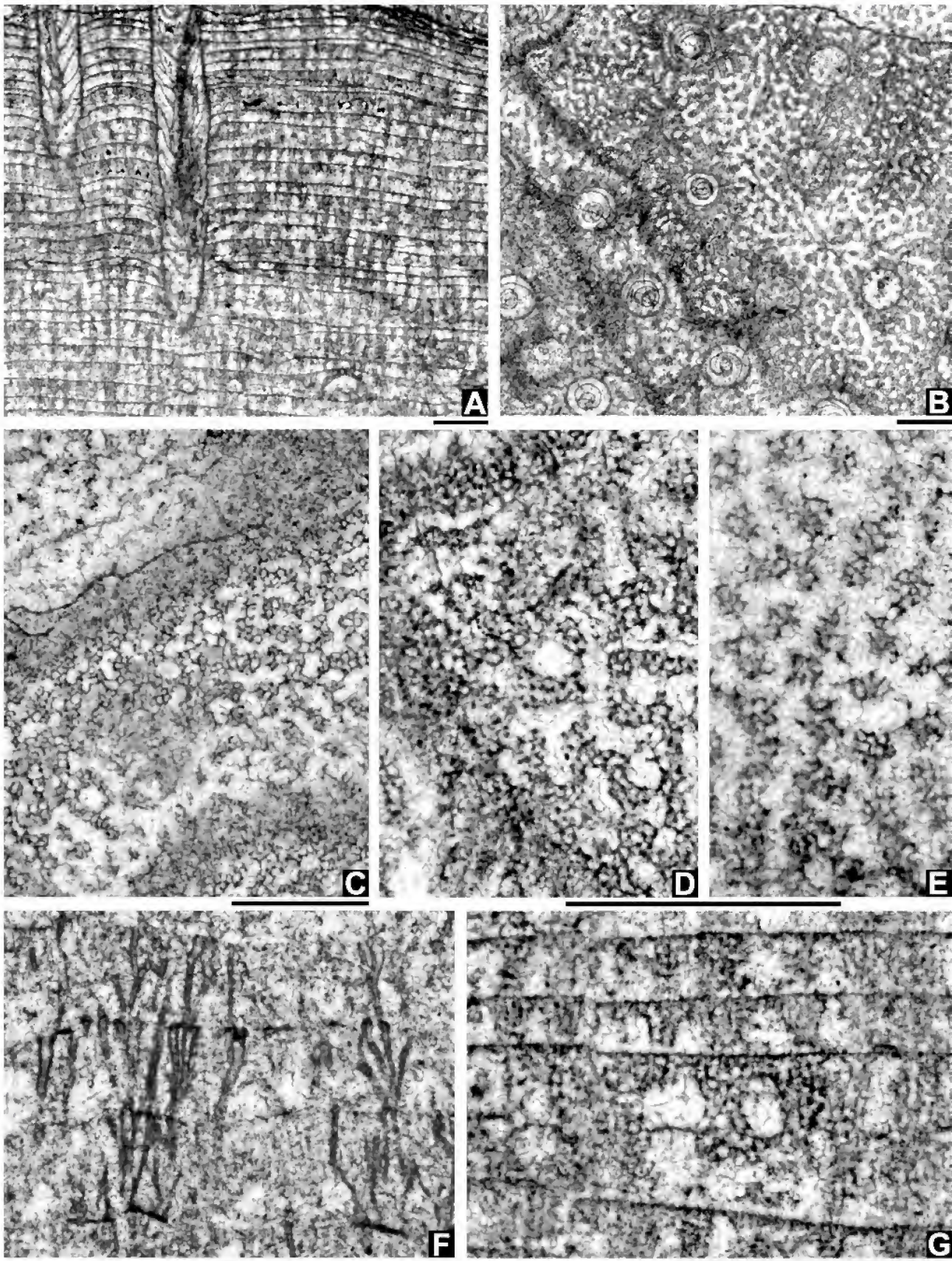


Fig. 5. *Atopostroma protentum* n.sp., A, B, D, G, holotype AM F.134892 from Martins Well Limestone Member (Shield Creek Formation), 1 m above base of MW section; (A, B), longitudinal (AM FT.15095) and tangential (AM FT.15096) sections, showing astrorhizae and associated caunopore tubes, $\times 10$; (C, E), tangential sections of paratype E, AM F.134897 (AM FT.15100), from Martins Well Limestone Member, 6 m above base of MW section; (C), showing characteristic morphological ... [continued on facing page]

structures) or may be separated by floors formed by dissepiments; most typically, however, pachysteles are regularly superposed (rarely branching) through up to 15 successive microlaminae, i.e., for distances of up to 3.5 mm, and have spacing ranging from 6 to 9 in 2 mm laterally. Microreticulation of pachysteles shown by slightly inclined upward and outward rows of micropillars and microcolliculi that define microgalleries; variation in sizes and shapes of microgalleries suggest irregular, acosmoreticular microstructure; usually microgalleries range from about 0.03 to 0.04 mm, rarely to 0.05 mm across; sometimes aligned rows of tiny melanospheric dots occur, possibly representing points where micropillars and microcolliculi intersected in their original state prior to diagenetic alteration. Between pachysteles, spar-filled gallery spaces tend to be upwardly elongated and slightly narrowing, about 0.1 to 0.2 mm across, with domelike tops in contact with upper microlaminae, and typically divided in two by a thin, wavy microlamina-like dissepiment; in these areas microlaminae do not exhibit larger pores but microreticular-sized pores may have existed but no longer clearly preserved in longitudinal sections.

In tangential section, lower parts of “interlaminar” spaces show isolated, rounded to irregular pachysteles from 0.15 to 0.2 mm in diameter within open spar-filled gallery spaces (Fig. 5C,E), and these grade into more elongate to vermicular pachystele shapes a little higher up within more sinuous gallery spaces, some of which probably represent traces of astrorhizal canals (Fig. 5D); pachystele margins in these lower-middle parts of “interlaminar” space are typically frayed (Fig. 5E), due to cut ends of beam-like microcolliculi; microgalleries vary from 0.03 to 0.05 mm across, and from shapes of microgalleries are evidence of acosmoreticular microstructure. In upper parts of “interlaminar” spaces, pachysteles become more coalesced though small, rounded spar-filled gallery spaces remain in places, from 0.10 to 0.15 mm in diameter. Closer to upper microlamina, skeletal material is almost entirely microreticulate, composed of rounded micropillars, 0.02 mm in diameter, and very fine rod-like microcolliculi, 0.007 mm thick, that define microgallery margins, typically 0.03 to 0.04 mm across. A gradational change occurs into darker, and more densely, microreticulated areas of upper microlamina, though microgallery dimensions remain much the same (Fig. 5D); also in a few places microgalleries seem to have become aligned and interconnected in arrangements that appear like slightly sinuous, very fine, tubule-like, pathways; however, in some, rather more dense and diffused areas the primary microreticulation of a microlamina has become

rather obscure (Fig. 5C), possibly owing to its diagenetic alteration into a more continuous, solid sheet with scattered dark ?melanospheric specks.

Remarks. *Atopostroma protentum*, though it bears close similarities to the type species *A. tuntouense* Yang & Dong, 1979 from the early Emsian of South China, especially in the spacing of tangentially directed structural elements (called “laminae” in the type species but appearing more like microlaminae), but exhibits differences in the longitudinally orientated elements (called “pillars” in the type species) with thicker, slightly wider spaced, and more continuously superposed structures than in the equivalent pachysteles of *A. protentum* n.sp. The present material is also comparable with the type material of *A. distans* (Ripper, 1937) from the Buchan Caves Limestone of Victoria (Webby *et al.*, 1993), material from the Jesse Limestone of New South Wales (Webby & Zhen, 1993), and also, as described from the Broken River area, herein, but *A. protentum* n.sp. as described here has slightly coarser, though less continuously superposed longitudinal structural elements; the pachystele spacing is from 6 to 8 in 2 mm in *A. protentum*, whereas in the Victorian type material of *A. distans* it is 8 to 9 in 2 mm; also dissepiments are comparatively uncommon in *A. distans*, and certainly none of the longer, microlamina-like dissepiments present in *A. protentum*. In addition the tangential structural elements of *A. protentum* are comparatively thinner (composed mainly of microlaminae) and more widely spaced, whereas the “laminae” of the Victorian type specimens of *A. distans* are relatively thicker and more closely spaced.

Comparisons with *A. stearni* n.sp. are also warranted especially as both *A. stearni* and *A. protentum* come from the same locality and horizon in the Martins Well section. The two species have many structural microstructural similarities, but *A. stearni* exhibits markedly different successional patterns of spacing of microlaminae; first, a closely spaced phase that includes a very limited development of pachystele structural elements, only some very short, rather scattered, micropillars; and secondly, a wide-spaced phase that includes a full range of longitudinally orientated features, such as upward-flaring pachysteles with acosmoreticular microstructure, and wavy, microlamina-like dissepiments. Examples of the close-spaced phase with sets of up to four microlaminae occur at irregular intervals through the skeleton. In contrast, *A. protentum* is dominantly composed of the wide-spaced phase of development—it mainly lacks developments of clustered close-spaced microlaminae. Also

Fig. 5 [continued from facing page] ... succession (and microreticulation) across one interlaminar area (AM FT.15106), with sharp contact between dense, more diffused and coalesced, pachystromal layer and “open”, irregularly rounded, pachystele profiles at base (see also Fig. 5E), then grading successively into an interconnected, anastomosing pachystele meshworks of middle to upper parts, and then into the next dense and diffused pachystromal layer at the top, $\times 25$; (D) tangential section of holotype (AM FT.15096) showing in greater detail the nature of the acosmoreticular microstructure in both more open, anastomosing pachystele network areas and darker, more diffused and dense pachystromal (or microlaminar)—in both areas dark, rounded, micropillars and interconnected microcolliculi are visible defining the microgalleries, $\times 50$; (E) tangential section of paratype E (AM FT.15106), showing detail of irregularly rounded, internally microreticulated pachystele profiles, and the frayed spine-like margins where ends of the beam-like microcolliculi have been intersected in tangential section, $\times 50$; (F) longitudinal section of paratype C, AM F.134895 (AM FT.15101), also from 6 m above base of MW section, showing the presence of a dendroid intergrowth of dark thread-like filaments that are internally differentiated into single rows of cells—it probably represents a new, as yet unnamed, cyanobacterium that infested parts of the microreticulate skeleton, spreading upwards and budding regularly longitudinally within the pachystele microgallery meshwork as well as becoming locally concentrated tangentially within successive pachystromal microgallery spaces, $\times 50$; (G) longitudinal section of holotype (AM FT.15095) shows pachysteles with well defined acosmoreticular to clinoreticular microstructure and the pachystromes are represented by dark, laterally persistent, regular microlaminae—they rarely show breaks in continuity, $\times 50$. All scale bars = 1 mm.

overall, *A. stearni* exhibits a closer spacing of pachystromes, on average between 12 and 17 in 2 mm, compared with *A. protentum* that shows a spacing of pachystromes, averaging between 7 and 8 in 2 mm.

Habrostroma Fagerstrom, 1982

Type species. *Stromatopora proxilaminata* Fagerstrom, 1961.

Discussion. In the type species of *Habrostroma*, *H. proxilaminatum* (Fagerstrom, 1961), Prosh & Stearn (1996, p. 36) described the pachystele microstructure as “orthoreticular to clinoreticular” in longitudinal section, and as having a “cellular (=irregular microreticular)” microstructure, presumably the “acosmoreticular” type of Stock (1989) in tangential section. However, other writers have recognized the genus *Habrostroma* as exhibiting only acosmoreticular microstructure (see Stock, 1991, 1997; Webby *et al.*, 1993). For comparative purposes, the genus *Atopostroma*, based on *A. tuntouense* Yang & Dong, 1979, has been described as exhibiting “orthoreticulate to clinoreticulate” microstructure (see Stearn, 1993, Stearn *et al.*, 1999), but also in Stearn (1990, p. 498) and Stock (1997, p. 549), as only exhibiting a clinoreticular type of microstructure, as in *Columnstroma* and *Coenostroma*, respectively. In the present study, the species of *Atopostroma* show examples of both acosmoreticular and clinoreticular microstructural types; no orthoreticular types have been found.

The diagnostic features of the two genera are as follows: *Habrostroma* typically has pachysteles that are shorter, more irregular, confined largely within “interlaminar” spaces (rarely superposed) and internally composed of an irregular network of acosmoreticulate skeletal material; and the pachystromes prominent but not thick, with one or more microlaminae, and sometimes microlamina-like dissepiments. *Atopostroma*, on the other hand, has pachysteles that are typically superposed, formed by upward and outward accretion to produce irregularly spread network of acosmoreticular to clinoreticulate skeletal material beneath successive, laterally extensive, microlaminae. The two described species *H. alternum* and *A. protentum* occur together in the Martins Well Limestone Member and are truly transitional forms, showing some features characteristic of each genus. Some consideration has been given to combining them, even treating them as different species of the one genus. However, between the mid-range and extremes of variation of the two species they are clearly representatives of different genera.

Habrostroma alternum n.sp.

Fig. 6A–F

Material. Six specimens including holotype MW6-3 (AM F.134908, AM FT.15128, AM FT.15129), and five paratypes MW1-2 (AM F.134909, AM FT.15130, AM FT.15131—paratype A), MW1-6 (AM F.134910, AM FT.15132, AM FT.15133—paratype B), MW1-12 (AM F.134911, AM FT.15134, AM FT.15135—paratype C), MW6-5 (AM F.134912, AM FT.15136, AM FT.15137—paratype D) and MW6-15 (AM F.134913, AM FT.15138, AM FT.15139—paratype E), from Martins Well Limestone Member, Shield Creek Formation (late Lochkovian-early Pragian) of the MW section of Mawson *et al.* (1988) near Martins Well; holotype as well as paratypes D and E are from 6 m above base of MW section, and the other paratypes, are from 1 m above base of section. Five other specimens MW1-3 (AM F.134914, AM FT.15140, AM FT.15141), MW1-8 (AM F.134915, AM FT.15142, AM FT.15143), MW1-19 (AM F.134916, AM FT.15144, AM FT.15145), MW6-19 (AM F.134917, AM FT.15146, AM FT.15147) and MW6-21 (AM F.134918, AM FT.15148, AM FT.15149) from the same locality, with the first three listed specimens from 1 m above base, and the last two, from 6 m above base of section.

Derivation of name: Latin, *alternum*, other—relating to the transitional relationships that exist between this taxon and *Atopostroma protentum* n.sp.

Diagnosis. A species of *Habrostroma* with pachysteles relatively short, mainly irregular but sometimes tending to be somewhat upwardly expanded; not usually superposed (and continuous) through more than about five successive pachystromes though more extended local alignments exist, but the related pachysteles are usually incomplete structures, that do not cross entirely each successive pachystrome; pachystromes are spaced moderately widely, from 5 to 14 in 2 mm (usually 8 to 9 in 2 mm); each has a prominent, extensive, thin, gently undulating, microlamina at top, and has irregular microreticular meshwork, including complete and incomplete pachysteles immediately below; between successive pachystromes, laterally extensive patterns of thin, wavy, microlamina-like dissepiments are commonly developed and often act as pachystele floors; microstructure acosmoreticular.

Description. Skeleton is domical with growth surfaces smooth to broadly undulate; latilaminae rarely seen, but discontinuity surfaces occur (Fig. 6A). Caunopore tubes of syringoporiid tabulate coral affinity commonly seen in intergrowth relationships (Fig. 6B,C,E); characteristically coral has deeply concave tabulae, and corallites usually have larger (0.7 to 0.85 mm) or smaller (0.3 to 0.55 mm) diameters; and in a few places lateral buds seen in smaller

Fig. 6 [continued from facing page] ... well defined more densely microreticulated microlaminae—also astrorhizal canals are conspicuous and caunopore tubes of two markedly different diameters occur, $\times 25$; (D) tangential section of paratype A, AM F.134909 (AM FT.15130), from the Martins Well Limestone Member (Shield Creek Formation), 1 m above base of MW section, showing acosmoreticular patterns of microstructure with locally well developed rounded micropillars and thin, beam-like microcolliculi, $\times 35$; (E) longitudinal section of holotype (AM FT.15128), showing pachysteles that are acosmoreticular, mainly confined within interlaminar spaces (rarely superposed) and have long, cyst-like interlaminar dissepiments, $\times 25$; (F) longitudinal section of holotype (AM FT.15128), showing greater detail with postlike to downward tapering pachysteles that tend to be confined to middle-upper parts of interlaminar spaces, even sometimes appearing to have their floors disrupted or commencing on the tops of the long, wavy, cystlike dissepiments, $\times 50$. All scale bars = 1 mm.

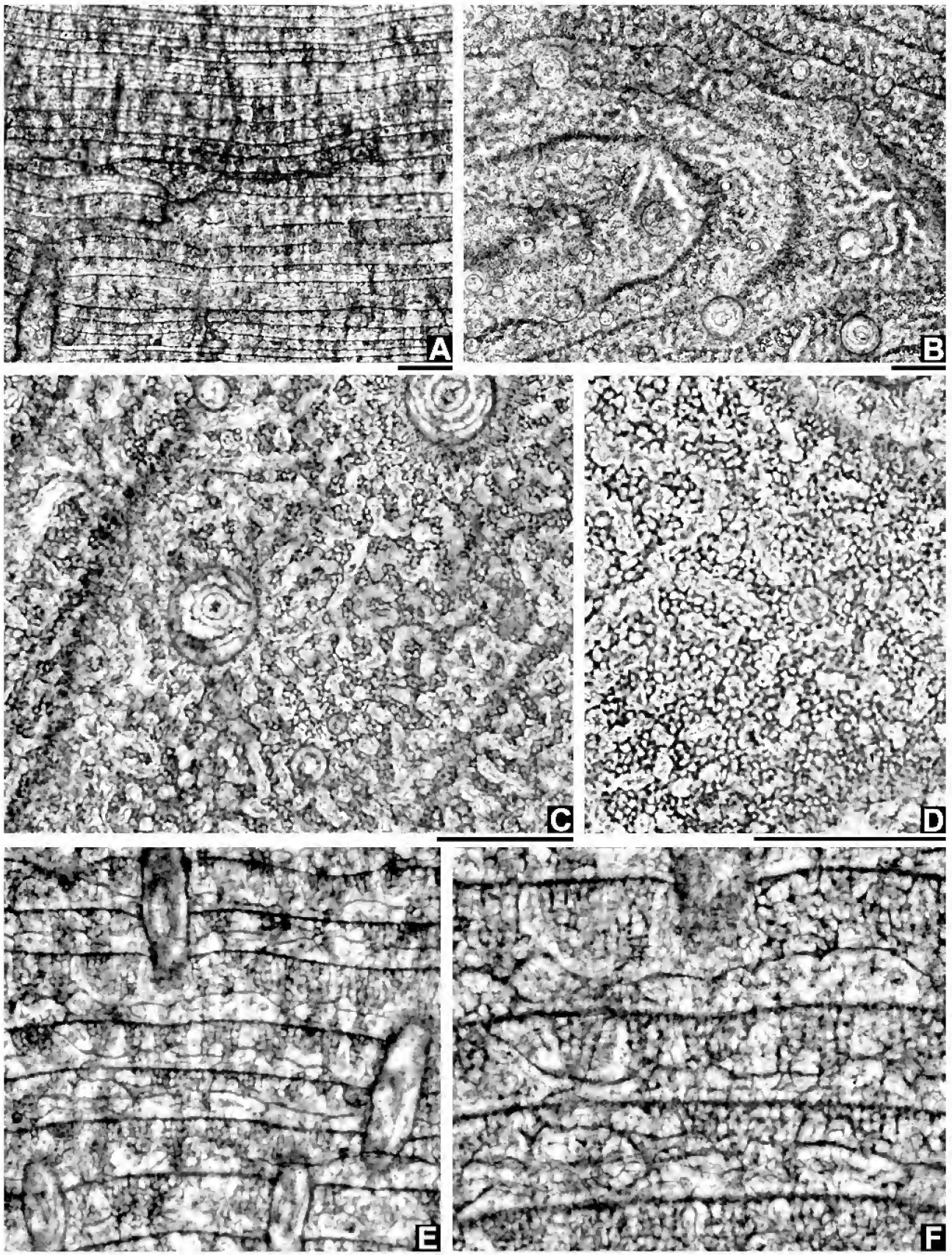


Fig. 6. *Habrostroma alternum* n.sp., A–C, E, F, holotype AM F.134908 from Martins Well Limestone Member (Shield Creek Formation), 6 m above base of MW section; (A) longitudinal section (AM FT.15128), $\times 10$; (B) tangential section (AM FT.15129), $\times 10$; (C) tangential section of holotype (AM FT.15129), showing nature of morphology and microreticulation across one interlaminar area, of mainly interconnected anastomosing acosmoreticular pachystele meshworks between the successive, narrow, ... [continued on facing page]

corallites; also rare solitary rugosans, and possibly a 0.3 to 0.4 mm diameter worm tube (possibly *Helicosalpinx*) occur. Astrorhizae only conspicuous in tangential section (Fig. 6B,C) forming localized stellate clusters of irregularly radiating and branching astrorhizal canals, spaced from 4 to 9 mm apart; and individual astrorhizal canals from 0.01 to 0.02 mm wide; in a few places, one or more converge into a single, untabulated, vertical canal, 0.02 to 0.03 mm in diameter, and sometimes associated with small mamelons, 0.5 mm wide and 0.8 mm high.

Single, thin, dark, laterally continuous, flattened to weakly undulate microlaminae are most conspicuous skeletal elements in longitudinal section; where in contact with caunopore tubes microlaminae almost always gently downflexed; only in a few places are close-spaced, second or third microlaminae seen to split off (or coalesce with) a microlamina; widest spacing between successive microlaminae is 0.6 mm; spacing more usually about 0.25 mm; spacing of microlaminae on average between 8 to 9 in 2 mm; spacing extremes range from 5 to 14 in 2 mm; microlaminae typically 0.025 mm thick and where a close-spaced pair of microlaminae develop they may be accompanied by traces of short micropillars, defining a row of microgalleries, each about 0.03 to 0.05 mm across; also a few small pores (foramina) may interrupt lateral continuity of microlaminae, from 0.07 to 0.15 mm in diameter.

Overall pachysteles rather short, irregular and not commonly radially aligned through skeleton; may extend across "interlaminar" spaces, as irregularly post-like or tapering downward structures, but are sometimes shorter, confined to upper two-thirds of "interlaminar" space (Fig. 6E,F); lower part is represented by poorly differentiated, spar-filled areas of galleries, astrorhizae and/or allotubes; in places where superposed, pachysteles occur they only extend for short distances to about 2 mm longitudinally; pachysteles are prominently microreticulate (largely acosmoreticular), and they are consistently spaced from 7 to 9 in 2 mm; individually pachystele dimensions are from 0.10 to 0.05 mm wide in lower part of interlaminar space to up to 0.25 mm wide in upper part; microgalleries are of irregular shape and size, with alignment of rows appearing to be orientated directly upward near axes of pachysteles but more splayed upward and outward towards pachystele margins.

"Interlaminar" spaces, especially in lower two-thirds, commonly exhibit small, thin, oblique to convex upward vesicle-like dissepiments, and more extended, undulating, microlamina-like dissepiments (Fig. 6E,F), that subdivide spar-filled gallery spaces and sometimes are also continuous through pachysteles; at tops the subdivided gallery spaces have dome-shaped outline, and usually 0.1 to 0.2 (rarely to 0.3) mm wide; they may extend up to overlying microlamina but are sometimes separated immediately beneath by a thin laterally spreading veneer of microreticulated skeletal material.

In tangential section towards the base, pachysteles composed of microreticulate skeletal material within rounded to irregular profiles, ranging from 0.05 to 0.20 mm in diameter (Fig. 6C,D); pachysteles tend to show frayed margins where beam-like microcolliculi are intersected; astrorhizal canals seem to mainly occupy more open vermiform areas; pachysteles coalesce into more completely closed networks towards tops; microlaminae are represented by darker, dense, rather diffused layers that still seem to show

many differentiated microgalleries.

In general microstructure is coarsely ascosome-like (Fig. 6C–F), with networks of irregular microgalleries, only crudely arranged in longitudinal and tangential rows, and ranging in most areas from 0.05 to 0.075 mm across, but may be smaller, down to 0.035 mm across, or exceptionally in places up to 0.1 or 0.15 mm across; micropillars rounded, about 0.01 mm in diameter, and may be from 0.02 to 0.03 mm apart in areas where more enclosed networks occur; in less well preserved areas appear to be replaced by darker melanospheric specks; areas of intersected microlaminae exhibit a finer microreticulation of microgalleries, usually about 0.025 mm in diameter.

Remarks: *Habrostroma alternum* shows features that are transitional to typical *A. contentum* but remains confidently referable to *Habrostroma*. It differs in exhibiting shorter and more irregular pachysteles and localized undulating microlamina-like dissepiments, though some characteristics of *Atopostroma* are also shown, such as the superposition (only partial) of pachysteles, and tendency for pachystele skeletal material to upwardly and outwardly veneer undersurfaces of successive microlaminae. *Habrostroma alternum* has little close resemblance to other known species of *Habrostroma* from Lower Devonian successions. In comparison with *H. tyersense* Webby, Stearn & Zhen, 1993 from the Pragian Cooper Creek Limestone and equivalents of Victoria, the Broken River species has pachystromes composed mainly of single microlaminae at tops of "interlaminar" spaces, rather than paired or multiple microlaminae with associated rows of microgalleries as in *H. tyersense*, and it also differs in having coarser and more widely spaced pachysteles as well as localized, microlamina-like dissepiments. *Habrostroma centrotum* (Girty, 1895) from the Manlius and Coeymans formations (Lochkovian) of New York (USA) as revised by Stock (1991, 1997) also exhibits some similarities, such as the presence of some localized, undulating, microlamina-like dissepiments, but pachysteles in *H. centrotum* are more continuously superposed and their laminae (or pachystromes) are more closely spaced. Another species, previously referred to as *Habrostroma* sp., from the Jesse Limestone (Emsian) of central-western New South Wales (Webby & Zhen, 1993), is probably closer to *Parallelopora* Bargatzky, 1881, than to *Habrostroma*.

Columnostroma Bogoyavlenskaya, 1972

Type species. *Coenostroma ristigouchense* Spencer, 1884, p. 599.

Columnostroma sp.

Fig. 7A–C

Material. Available material is fragmentary and recrystallized, comprising two specimens, SD260-11-3 (AM F.134919, AM FT.15150, AM FT.15151) and SD260-11-4 (AM F.134920, AM FT.15152, AM FT.15153, AM FT.15154), from 11 m above the base of the Dosey Limestone in SD260 section of Sloan *et al.* (1995), 2 km NNW of Storm Hill; the latter specimen is somewhat better preserved.

Description. Skeleton laminar to weakly mamelonate and latilaminar; dominated by long, thickened and radially aligned pachysteles, 0.2 to 0.35 mm across, with spacing from 3 to 5 in 2 mm; commonly they are close spaced, and often in contact, but rarely seen to merge or branch; because of alteration, pachysteles are preserved mainly as compact, dense, rod-like elements, but a few aligned dark melanospheric dots are preserved confirming an incomplete microreticulation of micropillars and microlaminae, from 0.02 to 0.03 mm thick, defining subrounded microgalleries about 0.04 to 0.05 mm in diameter. Pachystromes are irregularly developed between pachysteles; they may be represented as thicker pachystromal extensions about 5 mm in length and up to 0.2 mm in thickness, but in other areas represented by short lengths of a poorly differentiated network that may include one or more microlaminae; they may be inconsistently aligned laterally, and much interrupted by intervening allotubes. Typically allotubes are elongated to rather irregular, and divided by slightly domal to obliquely aligned dissepiments, at intervals of 10 to 15 in 2 mm longitudinally; in tangential section allotubes are small and circular in outline, about 0.2 mm in diameter. Astrorhizal canals may be centred in broad mamelons, their branches extend tangentially through other parts of skeleton; some exhibit tabulae from 0.2 to 0.4 mm apart.

Remarks. The Broken River species should probably be assigned to the genus *Columnostroma* on the basis of its long, stout, rounded, close-spaced pachysteles, less important pachystromes and traces of a fine reticular microstructure, though the particular type of microreticulation, *sensu* Stock (1989), cannot be ascertained. However, owing to the incompleteness of available material and poor preservation overall, the species must be left in open nomenclature. The type species of *Columnostroma*, *C. ristigouchense* (Spencer, 1884) from the Early Devonian of New Brunswick, Canada, shows some resemblances, having rather similar overall dimensions, but the pachysteles of the Broken River species are slightly thicker and more closely spaced, and the laminae within pachystromal segments are not demonstrably colliculate. Only one Australian species of *Columnostroma*, *C. clathratum* Webby, Stearn & Zhen, 1993 has been described previously from the Pragian Lilydale Limestone of Victoria, and this bears little resemblance to the Broken River species, being much finer in overall skeletal structure, and the pachystromes more regular, continuous, and fine-textured, with microlaminae mainly in conformity with the horizontal dissepiments crossing the allotubes.

Family Parallelostromatidae

Bogoyavlenskaya, 1984

Parallelopora Bargatzky, 1881

Type species. *Parallelopora ostiolata* Bargatzky, 1881.

Parallelopora sp.

Fig. 7D,E

Material. Two specimens, UQF.47983 and UQF.47979, both from UQL.2974 in reworked pebbles of the Chinaman Creek Limestone (Broken River Group), South Chinaman Creek, north of abandoned Pandanus Creek Station (material collected by C.W. Mallett in the late 1960s).

Description. Skeleton dominantly of long, continuous, thickened, pachysteles composed of coarsely microreticulated material, and successive, moderately close-spaced and laterally extended, thin microlaminae; pachysteles usually from 0.25 to 0.35 mm thick in areas where allotubes or other gallery spaces are well developed, and typically spaced from 3 to 4 in 2 mm; adjacent pachysteles sometimes merge locally or branch, where no gallery spaces intervene as pachystromal intervals; up to 2.5 mm long and 0.025 mm thick but such relationships do not normally maintain marked longitudinal continuity. Flattened to gently undulant microlaminae are apparently diagenetic derivatives of regularly aligned microcolliculi, and have lateral continuity over distances of 6 mm or more (shorter where allotubes intersect them or a microlamina acutely divides); they appear mainly as thin, dark lines from 0.02 to 0.04 mm across, in a few places showing a line of dark melanospheric dots and in places showing small-scale disruptions in continuity that may represent pores; spacing of microlaminae from 10 to 13 in 2 mm. Allotubes are common in places, showing slightly elongated outlines (circular to subcircular in tangential section), 0.2 to 0.3 mm wide; only a few small, oblique to concave cyst-like dissepiments seen; astrorhizal canals common, usually elongated, vermiform or branching and, typically 0.25 mm in diameter; in addition a few larger, irregularly-shaped, near millimetre-size, gallery spaces occur.

Microstructure of pachysteles is coarsely microreticulate (seemingly orthoreticular), composed of microgalleries, 0.075 to 0.125 mm in diameter; they are typically an association of micropillars that seem to have coalesced into superposed, walled, radially-aligned, tubules, and crossed by microlaminae that seemingly bound tops and bottoms of microgalleries (not possible to determine whether they are micro-beams or floors); nevertheless they are thinner and noticeably less markedly regularly spaced, and imprinted than the microlaminae at tops and bottoms of "interlaminar" spaces.

Remarks. The Broken River species is referred to the genus *Parallelopora* but owing to its indifferent preservation cannot be assigned to a named species. The material was studied previously by C.W. Mallett (1968, p. 225) as part of an unpublished Masters thesis at University of Queensland. Mallett revised Lecompte's species of *Stromatopora laminosa* Lecompte, 1952 (p. 276) from the Givetian of Olloy, Belgium, as a representative of *Parallelopora* based on the differentiation of its fine compact microlaminae and pillars (=pachysteles) with an amalgamated and microreticulated skeletal framework and presence of "pseudozooidal tubes" (=allotubes). Furthermore, Mallett accommodated the Queensland material in Lecompte's species. However, the assignment of *S. laminosa* to *Parallelopora* remains in some doubt; for example, Stearn (1993, p. 222; and see species list in 24-page Supplementary Publication No. SUP 14042 deposited by Stearn in British Library, Boston Spa, Yorkshire, UK) regarded *S. laminosa* as a representative of the genus *Habrostroma*. For instance, the poorly preserved Broken River material does not show the characteristic short pachysteles of *Habrostroma*. In contrast, it does have coarsely microreticulated and extended pachysteles that are diagnostic features of *Parallelopora*.

Little close similarity exists between the Broken River species and other known Australian species of *Parallelopora*. *P. ampla* Webby, Stearn & Zhen, 1993 from the Emsian of

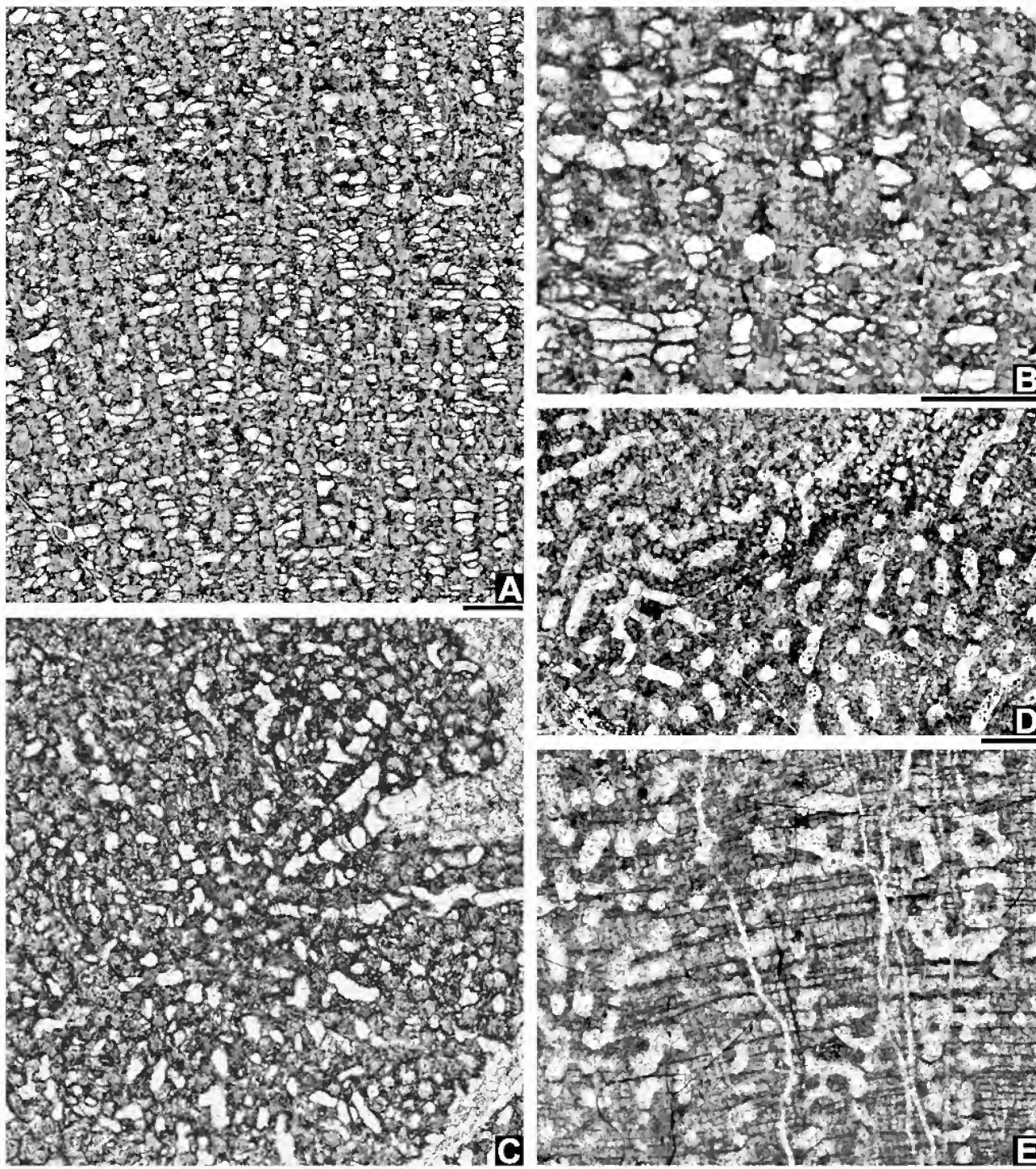


Fig. 7. *Columnnostroma* sp., A–C, specimen AM F.134920, from the Dosey Limestone, 11 m above the base of the SD260 section, NNW of Storm Hill; (A) longitudinal section (AM FT.15152), $\times 10$; (B) longitudinal section (AM FT.15152), showing within much thickened pachysteles small areas where incompletely aligned longitudinal rows of microgalleries and dark melanospheric rows of dots occur, confirming the poorly preserved microreticulation, $\times 20$; (C) tangential section (AM FT.15154), $\times 10$. *Parallelopora* sp., D, E, both specimens come from the same locality at UQL. 2974 of Mallett 1968, as reworked pebbles from Chinaman Creek Limestone along South Chinaman Creek; (D) tangential section of specimen UQF.47979, $\times 10$; (E), longitudinal section of specimen UQF.47983, $\times 10$. Scale bars = 1 mm.

the Murrundal Limestone of Victoria has much thinner pachysteles and only one or two longitudinally aligned rows of microgalleries in each pachystelete. Another species from the Middle Devonian lower Burdekin Formation of the Burdekin Basin (northern Queensland) was reported by Cook (1999, p. 542, fig. 57) as *?Parallelopora* sp. (though

Cook named it also as "*Parallelostroma* sp." in his caption to figure 57). It shows a closer relationship to the Broken River species with similarly spaced microlaminae, but the pachysteles are comparatively thinner, and astrorhizae do not appear to be present.

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